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RODENTS (MAMMALIA) FROM THE BARSTOVIAN (MIOCENE) ANCENEY LOCAL FAUNA, MONTANA

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ABSTRACT

Sixteen rodent species representing five families are recognized from the Barstovian Anceney local fauna of Montana. Of these, seven are new: one mylagaulid (*Trilaccogaulus bettae*), one sciurid (*Spermophilus jerae*), one castorid (*Euroxenomys inconnexus*), three heteromyids (*Mookomys thrinax, Peridiomys halis, Perognathus ancenensis*), and one cricetid (*Copemys lindsayi*). The fauna also contains the earliest known occurrence of *Cynomys,* otherwise unknown until late Hemphillian times. The heteromyid *Cupidinimus madisonensis* is shown to be distinct from *C. halli,* with which it had previously been synonymized.

Based on the rodents and associated fauna, the age of the Anceney fauna appears to be early Barstovian.

INTRODUCTION

The Madison Valley Formation is exposed in the Three Forks Basin of Montana. Douglass (1899, 1903, 1908, 1909) first worked this formation, collecting numerous fossil mammals. Douglass' collections were obtained primarily from the exposed cliffs along the Madison River (including the type section), but unfortunately his material was not accompanied by adequate stratigraphic data. The formation includes 172 m (564 ft) of accumulated sediments (Dorr, 1956), so the faunal elements can only be used in general correlations. The Madison Valley Formation was originally thought to be ?Arikareean–Clarendonian, but was later revised to include only the Barstovian–?Clarendonian interval. Dorr (1954, 1956) presented detailed discussions of the geology of the bluff areas along the Madison River.

In 1939 a field party from the Carnegie Museum of Natural History led by J. L. Kay discovered fossil remains in a roadcut near Anceney, Montana. Periodically after that date fossils were collected from this locality, but these were not studied in detail until much later, when Dorr (1956) designated the fauna the Anceney local fauna. He correlated the fauna and beds with the upper quarter of the Madison Valley Formation. Sporadic collecting at this site continued until 1971, when more intensive collecting took place.

Previously, eight species of mammals have been described from the Anceney local fauna (Dorr, 1956; Sutton and Genoways, 1974; Table 1). Different collecting techniques have significantly enlarged the micromammal component of this fauna, allowing description of 16 rodent species here.

The deposits are primarily channel accumulations of sands, gravel, clays, and

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Table 1.—*Previously cited mammalian species from the Anceney local fauna.*

- Chiroptera
  - Vespertilionidae
    - *Ancenycteris rasmusseni*
- Rodentia
  - Mylagaulidae
    - *Mesogaulus*? cf. *M. ballensis*
  - Castoridae
    - *Monosaulax pansus*?
  - Heteromyidae
    - *Perognathoides madisonensis*
- Carnivora
  - Mustelidae
    - *Martes* sp. indet.
    - *Hypsoparia bozemanensis*
- Perissodactyla
  - Equidae
    - *Merychippus* (*Protohippus*) near *M. intermontanus*
- Artiodactyla
  - Camelidae
    - gen. and sp. indet. (near *Rakomylus*)

tuffaceous materials. The locality is situated approximately 21 km (13 mi) west of Bozeman, Montana, in Gallatin County along Route 131 (center, N 1/2, sec. 13, T2S, R3E). It is the only area of exposures between Bozeman and Anceney, about 5 km (3 mi) east of the bluffs of the Madison Valley Formation that crop out along the east side of the Madison River.

Rodent dental terminology used below generally follows that of Wood and Wilson (1936) with modifications for the Geomyoidea proposed by Rensberger (1971, 1973), for the Castoridae proposed by Stirton (1935), and the Mylagaulidae (see Fig. 1). Abbreviations for dental measurements and statistics are given in Tables 2 and 5.

Abbreviations for institutions are: AMNH, American Museum of Natural History; CM, Carnegie Museum of Natural History; KU, University of Kansas Museum of Natural History; UCMP, University of California Museum of Paleontology, Berkeley.

SYSTEMATIC PALEONTOLOGY

Order Rodentia Bowdich, 1821

Family Mylagaulidae Cope, 1881

Genus *Trilaccogaulus* Korth, 1992

Trilaccogaulus bettae, **new species**

(Fig. 2, Table 2)

Holotype.—CM 27734, left fragment of mandible with P_4.

Horizon and Locality.—Anceney local fauna, center N 1/2, sec. 13, T2S, R3E, Madison Valley Formation, Gallatin County, Montana.

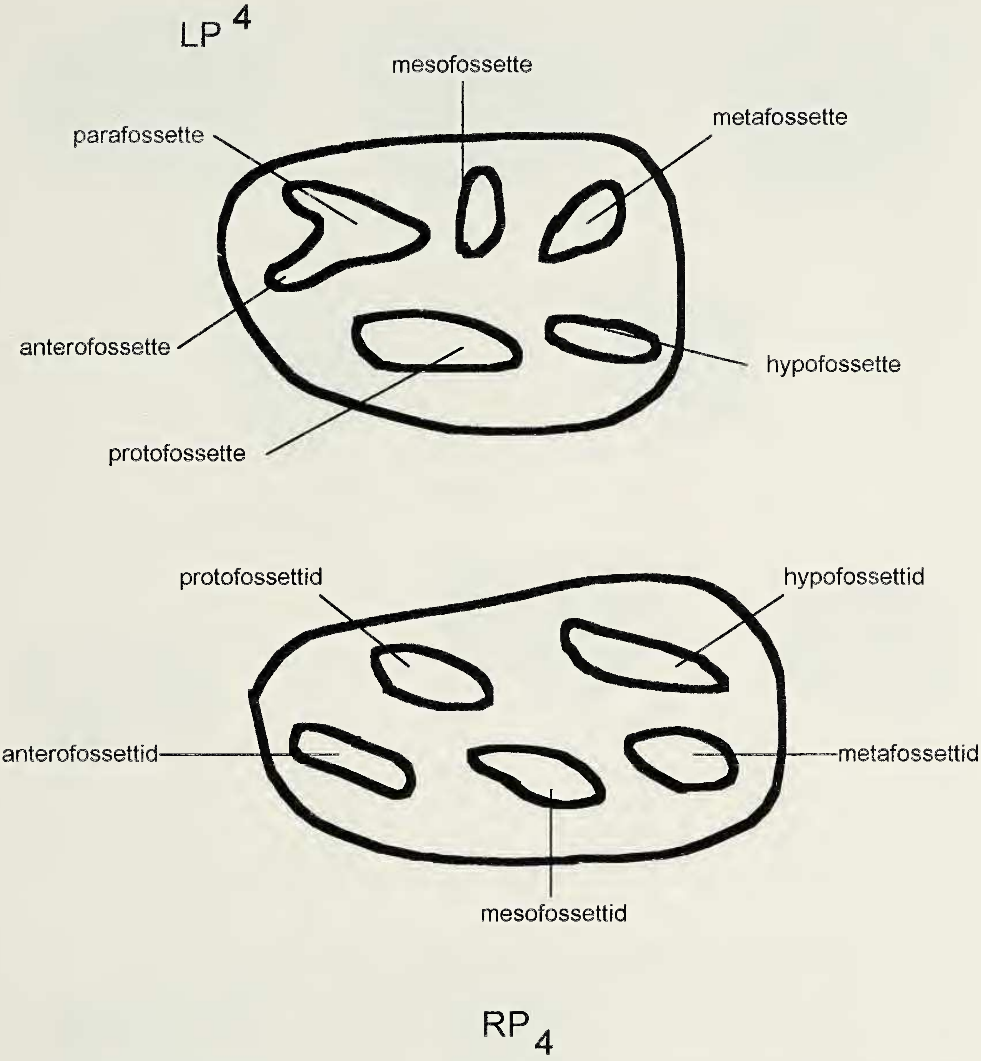

Fig. 1.—Schematic diagrams showing the dental nomenclature for the premolars of Mylagaulidae used in this text. Anterior is to the left of the page, lingual to the bottom of the page.

Age.—Early Barstovian (middle Miocene).

Referred Specimens.—CM 27742–27751, KU 28460–28464, dP^4; CM 27728–27733, KU 28453–28459, P^4; CM 27752–27759, KU 28434–28443, M^1; CM 27760–27771, CM 27773, KU 28418–28433, M^2; CM 27787–27791, M^3; CM 27798–27803, KU 28401–28402 dP$_4$; CM 27734–27741, KU 28444–28452, P$_4$; CM 27772–27778, KU 28415–28417, M$_1$; CM 27779–27786, KU 28405–28414, M$_2$; CM 27792–27797, KU 28403–28404, M$_3$.

Diagnosis.—Premolars much higher crowned than in other species; anteroconid on unworn P$_4$ closes off anterofossettid anteriorly (not open as in other species); protofossette and mesofossette of P^4 is retained until much later in wear than in other species.

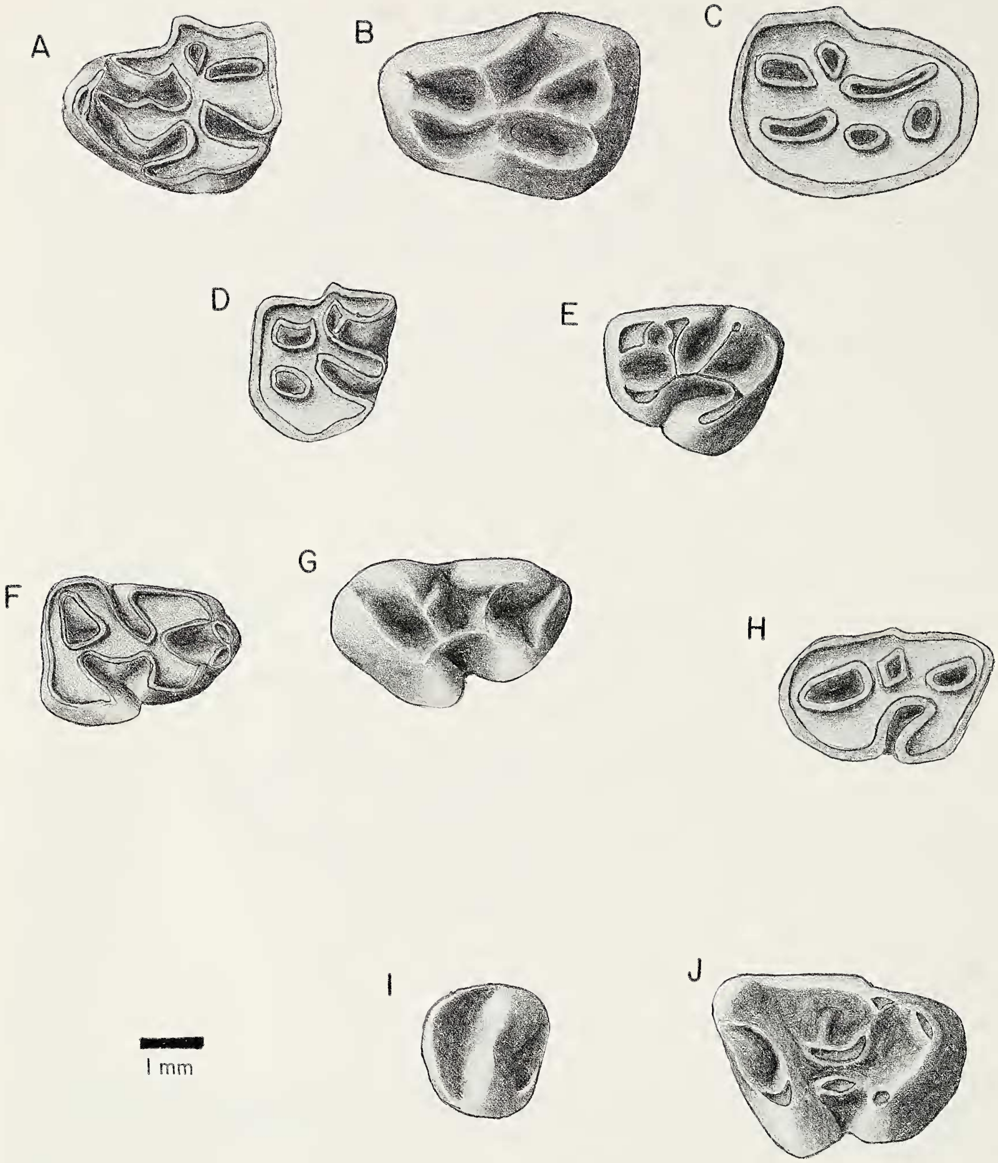

Fig. 2.—Cheek teeth of *Trilaccogaulus bettae* and ?*Cynomys* sp. A–H, *T. bettae.* A, left dP^4, CM 27750. B, left P^4, CM 27728. C, right P^4, CM 27733. D, left M^1, CM 27753. E, left M_1, CM 27773. F, right dP_4, CM 27801. G, right P_4, CM 27738. H, left P_4 (holotype), CM 27734. I–J, ?*Cynomys* sp. I, left P^3, CM 27843. J, left M_3, CM 27842.

Etymology.—Patronym for Elizabeth Hill of the Carnegie Museum of Natural History.

Description.—DP^4 is very low crowned and has a root under the anterocone, protocone, and metacone. Unlike that in P^4, the anterocone of dP^4 does not wear as quickly as the rest of the tooth, and the mesostyle is much more prominent. The mesofossette is sigmoid transversely but is shallow and disappears early in wear. The protofossette is either single or split into two fossettes.

Table 2.—*Dental measurements of* Trilaccogaulus bettae. *Measurements given in mm. Abbreviations: a-p, anteroposterior length; a-p(o), anteroposterior length of the occlusal surface; a-p(m), maximum anteroposterior length; tr, transverse width; tr(o), transverse width of the occlusal surface; tr(m), maximum transverse width. Statistical abbreviations:* n, *number of specimens;* $\bar{x}$, *mean; or, range of measurements;* s, *standard deviation; cv, coefficient of variation.*

		n	$\bar{x}$	or	*s*	cv
dP^4	a-p	15	2.94	2.65–3.22	0.17	5.74
	tr	14	2.60	2.48–2.89	0.13	5.07
P^4	a-p(o)	12	3.33	2.81–4.10	0.43	12.85
	a-p(m)	12	4.27	4.00–4.62	0.20	4.77
	tr(o)	12	2.32	1.87–2.94	0.36	15.38
	tr(m)	12	3.00	2.51–3.33	0.27	8.96
M^1	a-p	15	2.21	1.90–2.38	0.14	6.33
	tr	16	2.40	2.20–2.56	0.11	4.41
M^2	a-p	26	2.15	1.83–2.40	0.15	6.93
	tr	26	2.23	1.90–2.49	0.14	6.36
M^3	a-p	5	1.60	1.42–1.79	0.14	8.87
	tr	5	1.50	1.39–1.64	0.10	6.66
dP_4	a-p	8	3.05	2.91–3.25	0.13	4.36
	tr	8	2.03	1.84–2.22	0.13	6.50
P_4	a-p(o)	16	3.41	2.58–4.58	0.66	21.41
	a-p(m)	16	4.34	3.50–4.70	0.36	8.31
	tr(o)	16	2.11	1.84–2.74	0.24	11.42
	tr(m)	16	2.46	2.14–2.80	0.21	8.41
M_1	a-p	10	2.46	2.25–2.69	0.16	6.30
	tr	10	2.14	1.89–2.32	0.14	6.30
M_2	a-p	18	2.33	2.00–2.52	0.13	5.49
	tr	18	2.04	1.88–2.18	0.09	4.25
M_3	a-p	8	1.54	1.42–1.69	0.09	6.13
	tr	8	1.69	1.53–1.85	0.10	5.62

Except for the hypocone, the primary cusps and conules are all distinct in unworn P^4s. There is no evidence of a hypocone; rather, a large central protocone slopes toward the anteroloph and posteroloph. The paracone and metacone are joined to the protoconule and metaconule respectively by narrow crests and the protoconule is weakly joined to the protocone. All of these crests increase in width with wear and become broader connections, isolating the fossettes. A small mesostyle is variably developed on the labial margin of the tooth. As wear proceeds, the mesofossette is the first to form, followed by the hypofossette. With further wear the rest of the flexi close until there are five or six fossettes: three small posterior fossettes (mesofossette, metafossette, and hypofossette) and two or three anterior fossettes (an elongate parafossette, and an elongate protofossette which may divide into two separate small fossettes). In only one fragmentary specimen (KU 28459) has wear proceeded far enough to produce a Y-shaped parafossette.

The occlusal outline of M^1 is almost square with a distinct mesostyle that blends into the labial margin of the tooth in later wear. The early stages of wear show five fossettes, but in later stages the mesofossette is lost. The arrangement of cusps and conules is similar to P^4, but there is no anterocone. The tooth is noticeably wedge-shaped from crown to root. This structure presumably allows room for the erupting P^4 to eventually displace the tooth entirely. The two roots occur beneath the mesostyle and the posterior margin of the protocone, allowing more room anteriorly for P^4.

The occlusal pattern and wear of the second molar is similar to M^1, but M^2 is smaller in occlusal dimensions. Crown height is much greater than in M^1 and the tooth lacks the compressed roots. Instead, it is cylindrical in cross section, with the roots remaining open until late wear. The tooth is also slightly curved, so that the root is more posteriorly placed than the occlusal surface.

M^3s are reduced in size and occlusal pattern with a prominent protocone and paracone present on the anterior margin of the tooth. From this point a posterior crest slopes posteromedially to connect the two cusps. In some specimens a small dam isolates two fossettes on the tooth; in others the dam is not present and the two fossettes are not formed until late wear by the confluence of the bases of the protocone and paracone. Occasionally, there is a slight swelling on the posterolabial part of the descending crest which may be the remnant of a metacone.

DP_4 is similar to P_4 in all aspects of the occlusal surface. The crown height is very low and the pattern is quickly worn from the tooth. The two widely spread roots originate under the anteroconid and the posterolabial corner of the tooth.

The lower permanent premolar is oval in outline with lateral compression. A small anteroconid closes a pit between the subequal protoconid and metaconid in some specimens, while in others the anteroflexid remains open until later wear. The protoconid and metaconid are joined posteromedially, and a small metastylid is closely appressed to the metaconid. This metastylid is quickly worn away, leaving the appearance of an elongate metaconid. The hypoconid is low and compressed, blending with the posteroloph which terminates at the posteromedial border of the tooth.

In later stages of wear the flexids are closed, resulting in four fossettids: anterofossettid, mesofossettid, metafossettid, and hypofossettid. The hypofossettid is the last to close and remains open until very late in wear. The three remaining fossettids close after little additional wear and form an anteroposterior row of three lakes. In the holotype (CM 27734), P_4 is moderately worn and the hypoflexid is still open lingually.

M_1 is roughly rectangular in shape with the metaconid and associated metastylid being the highest point on the tooth. There is no anteroconid, and the protoconid and hypoconid are low. A small crest from the metaconid isolates a small ephemeral fossettid labial to the metastylid. This fossettid eventually becomes part of the mesofossettid with wear. The metaflexid opens posteriorly and the hypoflexid remains open until very late wear. The shape of the tooth modifies with wear due to the severe anteroposterior compression of the basal part of the crown and roots. As in M^1, the shape of M_1 allows for enlargement of the premolar with attrition.

M_2 is similar to M_1 in occlusal outline but is much higher crowned, with no constriction of the basal part of the crown or roots. In late wear the mesofossettid is lost and only the anterofossettid, hypofossettid, and metafossettid remain. The shape of the tooth varies little with wear and is essentially square, with the trigonid only slightly wider than the talonid.

The lower third molar is smaller than M_2 and is curved so that the root lies almost parallel to the occlusal plane. The metaconid and bulbous protoconid are separated by a small cuspule (?anteroconid) on the anterior margin of the tooth. This cuspule is usually united to the metaconid by a short crest and disappears with wear. Posteriorly, the talonid may be a single pit surrounded by a crest from the metaconid to the protoconid or it may be divided into fossettids.

Only two specimens preserve fragments of the jaw, the holotype (CM 27734) and a right mandible fragment with dP_4 (KU 28401). Both specimens are broken immediately behind and below the premolar, so jaw depth cannot be measured. CM 27734 has the diastema intact, which is relatively short and strongly recurved. The alveolus for the incisor indicates that it carried a rather stout tooth approximately 2.5 mm in diameter. The holotype is broken through the mental foramen so that only the dorsal margin of the foramen is intact. The mental foramen is slightly anterior to P_4 and posterior to the deepest part of the diastema. The foramen is well down the side of the jaw at the level of the roots of P_4. In KU 28401 the entire foramen is preserved and is widely oval in shape. The posterior part of the foramen is deep. Anteriorly, it shallows as a widely flaring groove coursing anterodorsally.

Discussion.—This species is clearly referable to *Trilaccogaulus* because of the simplified pattern of three persistent fossettids on P_4 (Korth, 1992). P^4 retains two additional fossettes (mesofossette and protofossette) that are lost in early stages of wear in all other species (also see Rensberger, 1979).

Trilaccogaulus bettae has markedly higher crowned premolars than any of the other species of the genus, approaching the crown height seen in species of *Mylagaulus. Trilaccogaulus bettae* also postdates all other species, the most recent being from the late Arikareean (Rensberger, 1979; Korth, 1992). Specimens similar in morphology to *T. bettae* are also present in the collections of the American Museum of Natural History from the earliest Barstovian Observation Quarry of Nebraska.

The species of *Trilaccogaulus* represent a distinct lineage of mylagaulids ranging from the early Arikareean to the early Barstovian, *T. bettae* being the youngest and most advanced species. Geographically, the occurrence of *T. bettae* is consistent with those of the Arikareean species known from the northern Great Plains and intermontane areas of Montana and Idaho (Nichols, 1976; Rensberger, 1979; Korth, 1992).

Genus *Mylagaulus* Cope, 1878
Mylagaulus vetus Matthew, 1924
(Fig. 3, Table 3)

Mesogaulus vetus (Matthew) Cook and Gregory, 1941.
Mesogaulus? cf. *M. ballensis* Riggs, Dorr, 1956.

Referred Specimens.—CM 8865, edentulous mandible; CM 27804, dP^4; CM 27805, P^4; CM 27806–27807, M^1; CM 27808, KU 28398, M^3; CM 27809, KU 28399, dP_4; CM 27810, KU 28400, P_4; CM 27811–27814, M_1.

Description.—The only specimen of P^4, CM 27805, is at a very late stage of wear. It is wider posteriorly than anteriorly and generally oval in shape. There is a thick cement band surrounding the tooth which thins on the posterior margin of the crown. On CM 27805, the cement is cracked away from the labial and part of the lingual margin of the tooth. The occlusal surface has six fossettes, with the protofossette being the largest and slightly sigmoid in shape. The parafossette is also long and is more arc-shaped, bowing out toward the labial border. A small anterior fossette (?anterofossette) is still present but is nearing exhaustion. On the posterolabial corner of the tooth the mesofossette and metafossette lie next to each other, with the metafossette extending anteriorly to the posterolabial margin of the parafossette. The hypofossette abuts the posterior end of the parafossette and extends posteriorly along the midline of the tooth.

A single dP^4 was recovered (CM 27804) and is only slightly worn. There is a prominent mesostyle, and the other primary cusps are distinct. Labially, the metacone is connected to the anterior margin of the metacone by a narrow crest, but it is not connected to any other crest or cusp in this early stage of wear. With wear it would join the short crest connecting the protocone and protoconule. The protoconule is also connected to the anterocone and the paracone by short crests. In the unworn tooth there are only four fossettes or flexi present: parafossette, protofossette, hypofossette, and metafossette. With wear it is evident that a small, central mesofossette will separate from the hypofossette. The tooth is low crowned, as would be expected from a deciduous tooth, with roots under the protocone, anterocone, and metacone.

Two M^1s with moderate wear were recovered (CM 27806 and CM 27807). These teeth are roughly square in occlusal outline with a large mesostyle. With wear, four fossettes are produced as well as a short-lived mesofossette, which unites with the parafossette with wear. The remaining fossettes (protofossette, metafossette, hypofossette) close relatively early in wear, with the metafossette being the last to close. The roots and basal part of the crown are anteroposteriorly compressed as in other species of mylagaulids. The mesostyle is persistent until late wear judging from its prominent ribbed structure which extends down to the roots.

M^3 is high crowned and curved posterolabially. Five fossettes are present in a moderately worn specimen (CM 27808) with a small protofossette and larger hypofossette. The metafossette, mesofossette, and parafossette are subequal in size and persist through later stages of wear, while the protofossette and hypofossette unite. A small mesostyle is discernible on the labial margin of the tooth, but is soon lost with wear.

DP_4 is relatively complex and low crowned. A prominent anteroconid is present on the anterior margin of the tooth connected to the high metaconid and lower protoconid. Immediately posterior to the protoconid is a small cusp (ectostylid) which is low and crest-like in CM 27809 but high and pillar-like in KU 28399. The metaconid is elongate and has a distinct metastylid on its posterior border. The entoconid is bilobed in the unworn state but becomes crest-like in later stages, as does the hypoconid. A single mure on the midline of the tooth starts at the protoconid–metaconid juncture and runs posteriorly to join the hypoconid, entoconid, and ectostylid. This mure would isolate five fossettids if wear proceeded further.

Two P_4s were recovered, one of which is quite worn (KU 28400) and the other showing moderate wear (CM 27810). In the worn specimen there are five fossettids: anterofossettid, protofossettid, mesofossettid, hypofossettid, and metafossettid. In CM 27810 there are six fossettids. Two small fossettids are about to join, forming the mesofossettid in later wear. In the lower premolars there is only a thin layer of cement on the outside of the teeth.

M_1 has anteroposteriorly constricted roots as does M^1, and the crown tapers toward the base of the

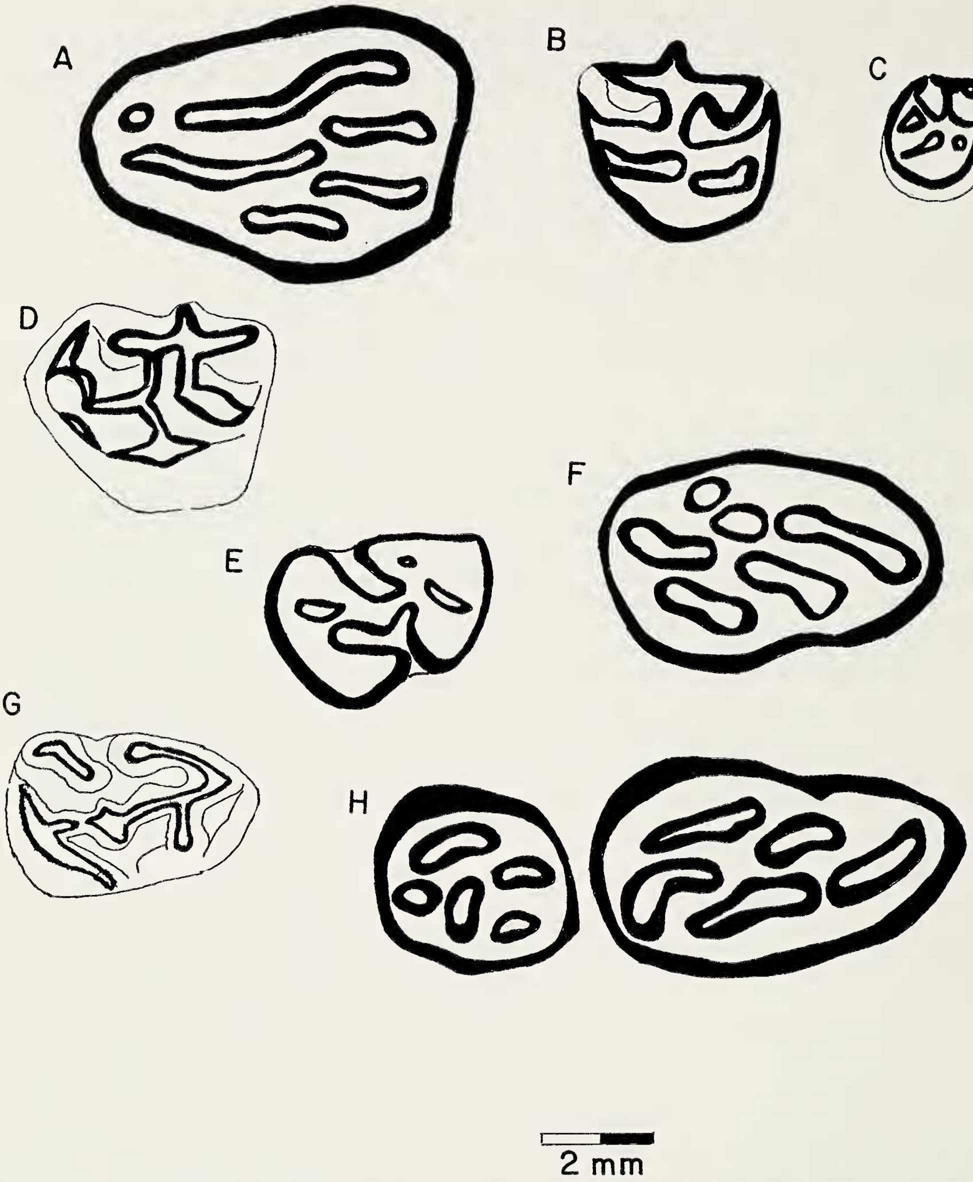

Fig. 3.—Cheek teeth of *Mylagaulus vetus*. A, left P^4, CM 27805. B, left M^1 or M^2, CM 27807. C, right M^3, CM 27808. D, left dP^4, CM 27804. E, right M_1, CM 27811. F, right P_4, CM 27810. G, left dP_4, CM 27809. H, right P_4–M_1, AMNH 18905 (holotype from Nebraska).

crown. The metaconid is the highest cusp and it slopes posteriorly, ending in a laterally compressed metastylid. There is no recognizable anteroconid on M_1. The anterofossettid is split into two fossettids in early wear but becomes joined in late wear. The protoflexid is forked and in one specimen (CM 27812) has become confluent with the metafossettid. Both the protoflexid and mesoflexid stay open until very late wear. CM 27814 differs from the other specimens in having a small ectostylid, a double metastylid, and a slight swelling anterior to the protoconid which could be the remnants of an anteroconid.

Table 3.—*Dental measurements of* Mylagaulus vetus. *Measurements in mm. Abbreviations as in Table 2.*

		a-p	tr
dP^4	CM 27804	3.90	3.26
P^4	CM 27805	6.80	5.55
M^1	CM 27806	3.24	—
	CM 27807	3.27	3.33
M^3	CM 27808	1.83	2.25
	KU 28398	2.29	3.05
dP_4	CM 27809	3.95	2.64
	KU 28399	4.21	—
P_4	CM 27810	7.75	4.00
	KU 28400	6.94	3.85
M_1	CM 27811	3.31	2.76
	CM 27812	3.40	2.85
	CM 27813	3.05	2.50
	CM 27814	3.36	2.57

Discussion.—The Anceney specimens can be referred to *Mylagaulus vetus* with confidence. An isolated P_4 (CM 27810) is nearly identical to P_4 in the holotype of *M. vetus,* AMNH 18905. The holotype is slightly more worn and therefore has slightly larger occlusal dimensions, but is comparable in its maximum measurements with CM 27810. The morphological difference between the holotype and the Anceney specimen is in the mesofossettid. In the holotype it is a single, elongate fossettid, whereas in CM 27810 it is two smaller fossettids. It appears that after wear these two small fossettids will fuse in the Anceney specimen, making it virtually identical to P_4 in the holotype.

Similarly, the P^4 from Anceney, CM 27805, is comparable in size and morphology to topotypic material of *M. vetus* from Nebraska. Due to the very late stage of wear of CM 27805, the fossettes are more anteroposteriorly elongate than in the less worn specimens from Nebraska, but the occlusal pattern is essentially identical to these specimens.

Black (1961) reported a single P^4 from the early Barstovian Flint Creek fauna of Montana that he referred to *Mesogaulus paniensis.* This specimen, CM 9564, is referable to *Mylagaulus vetus. Mesogaulus paniensis* differs from *Mylagaulus* predominantly in the occlusal pattern and outline of the premolars. Besides having fewer and less elongate fossettes, in all species of *Mesogaulus* the outline of P^4 maintains a discernible buccal projection (mesostyle) and a distinct lingual invagination on the anterolingual corner, outlining the anterocone (see Wilson, 1960: fig. 47–49). In contrast, the P^4s of *Mylagaulus* are nearly oval in outline, with little or no indication of distinct cusps. Lower premolars of *Mylagaulus,* like the P^4s, have more fossettids that are more elongate than do P_4s of *Mesogaulus.* Based on this distinction, *M. vetus* is the most primitive species of *Mylagaulus,* being more advanced than any *Mesogaulus* but more primitive than other Barstovian species of *Mylagaulus, M. laevis* and *M. monodon.*

Munthe (1988) described a skull, several mandibles, and numerous isolated teeth of *Mesogaulus vetus* from the late Hemingfordian Split Rock fauna of Wyoming. He referred this material to *Mesogaulus* rather than to *Mylagaulus,* following the admittedly arbitrary biostratigraphic boundary between the genera (Hemingfordian = *Mesogaulus*; Barstovian = *Mylagaulus*) established by earlier authors (Cook and Gregory, 1941). *Mylagaulus vetus* is clearly transitional in morphology between species of *Mesogaulus* (e.g., *M. paniensis*) and *Mylagaulus* (e.g., *M. laevis*). No diagnosis currently exists that clearly separates *Mesogaulus* from *Mylagaulus.* A complete review of the species of Mylagaulidae is necessary to determine the validity of the genera and species.

Douglass (1903) described two species of *Mylagaulus* from the Madison Valley Formation, Montana, based on single specimens: *M. pristinus* (CM 742) and *M. proximus* (CM 843). Black (1961) mentioned that possibly *M. paniensis* from Flint Creek (referred above to *M. vetus*), *M. pristinus,* and *M. proximus* were synonymous. The type of *M. pristinus* differs little from the Anceney specimens of *M. vetus,* except for some variations due to wear. The holotype of *M. proximus* is the mandible of an immature animal with P_4 unerupted, dP_4 roots still in place, and M_3 unerupted as well (Douglass, 1903:fig. 27). The structure of the preserved portions of the mandible of *M. proximus* is definitely that of an immature animal and differences in size and strength of the masseteric ridges can easily be accounted for on the basis of age. It is likely that these species are synonyms. If these species should be synonymized in the future, they would be referred to the senior synonym, either *M. pristinus* or *M. proximus* both named by Douglass (1903).

Family Sciuridae Gray, 1821
Subfamily Sciurinae Gray, 1821
Tribe Tamiini Moore, 1959
Genus *Tamias* Illiger, 1811
Tamias sp.
(Fig. 4, Table 4)

Referred Specimens.—CM 27846, 27847, P^4; CM 27848–27854, M^1 or M^2; CM 27855, M^3; CM 27856, P_4; CM 27857–27862, M_1 or M_2; CM 27863, M_3.

Description.—The upper teeth are similar to other *Tamias* teeth described from various Miocene deposits in North America and only a brief description will be given here. The upper premolar is triangular with well-developed metaconule, protoconule discernible on unworn teeth, and metaloph with weak connection to the protocone. The anterior and posterior cingula are short and there is a reasonably well-developed mesostyle. The upper molars are similar, with the cingula more expanded lingually, giving the teeth a more squared appearance. The metaloph is incomplete or only narrowly connected to the protocone, the metaconule is developed, and there is no distinguishable protoconule. M^3 is expanded posterolabially and there is no sign of a metaloph or metaconule.

P_4 is narrow anteriorly with the protoconid and metaconid closely appressed, reducing the trigonid basin to a slit which is lost with wear. The posterolophid is relatively straight, ending lingually in a small but well-defined entoconid. The lower molars are basically square with some rounding of the posterointernal corners of the teeth at the entoconids. The trigonids are closed on most specimens but open posteriorly on CM 27857. There are no mesoconids and only slight indications of mesostylids, which are lost with wear. CM 27863 is the only M_3 recovered, and it is extremely worn. It is elongate, being expanded mainly in the regions of the hypoconid and entoconid. The trigonid basin is closed.

Discussion.—The genus *Tamias* is used here rather than *Eutamias* as has been favored by a number of authors for middle Tertiary tamiines (Hall, 1930; Shotwell, 1970; Voorhies, 1990*a*) for biogeographic reasons. However, Recent species of *Eutamias* maintain P^3 in the upper dentition, whereas this tooth is lacking in species of *Tamias.* None of the P^4s referred to *Tamias* from Anceney have an interdental wear facet along the anterior edge of the tooth to accommodate P^3.

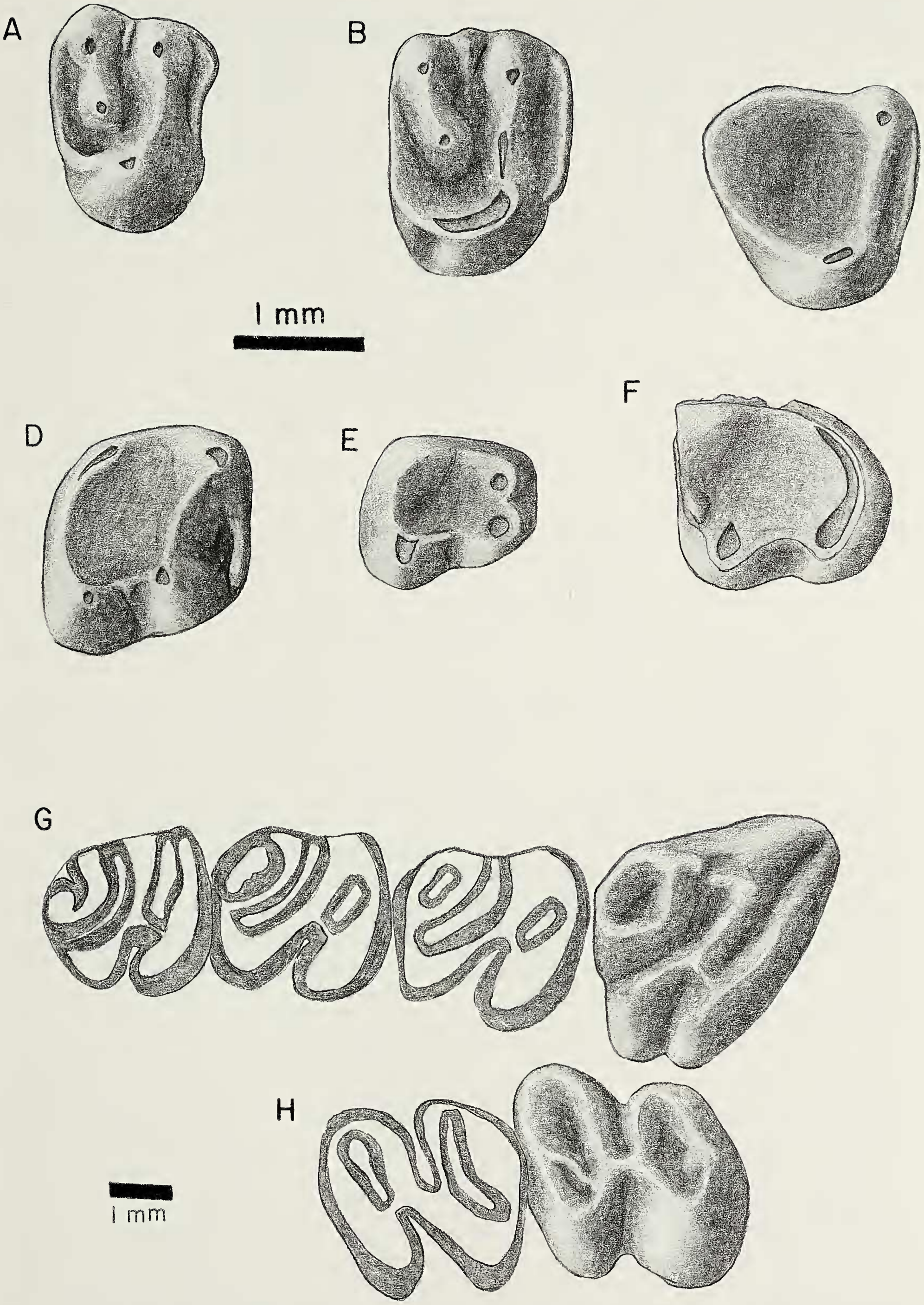

Fig. 4.—Dentition of *Tamias* sp. and *Euroxenomys inconnexus* from Anceney local fauna. A–F, *Tamias* sp. A, right P^4, CM 27847. B, right M^1 or M^2, CM 27848. C, right M^3, CM 27855. D, right M_1 or M_2, CM 27858. E, right P_4, CM 27856. F, left M_3, CM 27863. G–H, *E. inconnexus,* CM 8925. G, right P^4–M^3. H, right P_4–M_1.

Table 4.—*Dental measurements of* Tamias *sp. from Anceney local fauna. Measurements in mm. Abbreviations as in Table 2. Additional abbreviations: tra, anterior transverse width; trp, posterior transverse width.*

		n	$\bar{x}$	or	*s*	cv
P^4	a-p	2	1.24	1.23–1.24	—	—
	tr	2	1.65	1.61–1.69	—	—
M^1 or M^2	a-p	6	1.54	1.42–1.64	0.06	4.22
	tr	7	1.78	1.67–2.13	0.15	8.52
M^3	a-p	1	1.69	—	—	—
	tr	1	1.67	—	—	—
P_4	a-p	1	1.40	—	—	—
	tra	1	0.93	—	—	—
	trp	1	1.30	—	—	—
M_1 or M_2	a-p	6	1.45	1.38–1.53	0.05	3.53
	tra	5	1.46	1.33–1.54	0.07	4.86
	trp	6	1.58	1.48–1.68	0.07	4.22
M_3	a-p	1	1.72	—	—	—
	tra	1	1.63	—	—	—
	trp	1	1.47	—	—	—

Therefore, it is believed that none existed, making the material referable to *Tamias* rather than *Eutamias.*

Pratt and Morgan (1989) erected *Nototamias* and included *T. ateles* as a referred species. The majority of the differences cited by Pratt and Morgan as separating their new genus from *Eutamias* and *Tamias* were characters of the mandible and the number of roots on the lower molars (two in *Nototamias* and four in other tamiines). However, the mandible of *T. ateles* has never been reported, so these characters are not applicable, and there are four roots on the lower molars of the species (Pratt and Morgan, 1989:97), the four-rooted condition being a derived feature rather than a primitive one as suggested by Pratt and Morgan (Korth, 1992:101). Hence, *T. ateles* is retained here in *Tamias* rather than *Nototamias.* The lower molars of the Anceney *Tamias* are clearly four-rooted and therefore cannot be referred to *Nototamias.*

The specimens discussed here are slightly larger than the Hemingfordian specimens from Split Rock, Wyoming (Black, 1963; Sutton, 1972), which may be referable to *Nototamias.* They agree in having a reduced mesostyle and in the structure of the lower molars; however, the upper molars are more nearly square and the metaloph is not as well developed as in the Wyoming specimens. The constriction of the metaloph is a character found in many Recent species of chipmunks and in *T. ateles* (Hall, 1930; Black, 1963). *Tamias ateles* is from the Barstovian of California, close in age to the Anceney fauna. Although it is similar in size, *T. ateles* differs from the Anceney material in having larger mesostyles on the upper molars and a metaconule on M^3. The Anceney material probably represents a species distinct from *T. ateles,* but until additional and more nearly complete material is recovered for both *T. ateles* and Anceney *Tamias,* no new species can be named.

Tribe Marmotini Simpson, 1945
Genus *Spermophilus* Cuvier, 1825
Subgenus *Otospermophilus* Brandt, 1844
Spermophilus (*Otospermophilus*) *jerae*, **new species**
(Fig. 5, Table 5)

Holotype.—CM 27834, crushed skull with upper cheek teeth.

Referred Specimens.—CM 27835, crushed skull; CM 27836–27840, mandibles; CM 27844, partial postcranial skeleton.

Horizon and Locality.—Anceney local fauna, center N 1/2, sec. 13, T2S, R3E, Madison Valley Formation, Gallatin County, Montana.

Age.—Early Barstovian (middle Miocene).

Diagnosis.—Protocones narrow rather than rounded as in other species; unique combination of slightly elevated parastyles and low mesostyles on upper molars; masseteric fossa terminates under anterior roots of M_1, more posterior than in other species; M_1 less compressed than M_2 (molars identical in other species); P_4 with distinct protoconid and metaconid, not fused as in *S. primitivus.*

Etymology.—Patronym for Jere Sutton.

Description.—Both of the skulls representing this species are badly crushed and incomplete. The skulls appear lightly built with a relatively short rostrum and broad neurocranium. The only observable cranial foramina do not differ from those of other sciurids. The infraorbital foramen is compressed and slit-like. External to it is a prominent masseteric tubercle. The posterior palatine and posterior maxillary foramina are preserved on the holotype. The posterior palatine foramen is small and even with the anterior margin of M^3. The posterior maxillary foramen is large and nearly circular in outline but, because of breakage, it is uncertain whether it was enclosed laterally. The incisive foramen appears very short as in other sciurids but its actual length cannot be measured, again due to breakage.

The upper incisors are deeper (anteroposteriorly) than wide. The anterior enamel surface is gently convex with numerous minute longitudinal ridges. Enamel extends just slightly onto the lateral sides of the incisors.

P^3 is small and peg-like, with a small posterior cingulum. P^4 is smaller than the molars, somewhat anteroposteriorly compressed and triangular in occlusal outline. The protoloph is straight with no protoconule evident, and the metaloph curves anteriorly toward the protocone from the distinct metaconules but does not meet the protocone. The anterior cingulum is long and shelf-like, extending from the lingual margin of the protocone to the anteroexternal portion of the paracone. A low mesostyle is located close to the metacone.

M^1 and M^2 are similar to P^4 but are wider lingually, due primarily to the flared lingual margin of the posterior cingulum. This area is better developed on M^1 than M^2, giving M^1 an almost square occlusal outline. The mesostyles are low and somewhat closer to the paracone than to the metacone. The anterior cingula are well developed, ending labially in an elevated parastyle. The protoloph is straight but the metaloph is oblique to the protocone and slightly compressed as it joins the protocone. A small anteroposteriorly compressed metaconule is discernible in the metaloph, and there is no protoconule on the protoloph.

Anteriorly, M^3 is similar to the other two molars; however, the protoloph is not perpendicular to the lingual margin but rather slants posteriorly from the anterior face of the protocone. The anterior cingulum is well developed but not as wide as those of the anterior molars, and there is no distinct parastyle. M^3 is expanded posteriorly, with no evidence of a metacone or metaloph. The expanded posterior cingulum joins the protocone at a deep notch just posterior to the protocone.

The mandible is relatively slender with a shallow diastemal depression, although not as shallow as that in the Barstovian *Spermophilus primitivus* from Madison Valley (Bryant, 1945; Black, 1963). The diastema is long, ending at the level of the tooth row, and the mental foramen is slightly anterior to the midpoint of the diastema. The masseteric fossa is rounded anteriorly and terminates below the anterior end of M_1. The masseteric crests are well defined but are not heavy as in *S. primitivus.* The pit for insertion of the *masseter temporalis* behind M_3 is not as well developed as that of *S. primitivus.*

The lower incisor is similar to the upper incisor in cross section. The anterior enamel surface also has the numerous longitudinal ridges seen on I^1.

P_4 is wider posteriorly than anteriorly because the protoconid and metaconid are closely set, sepa-

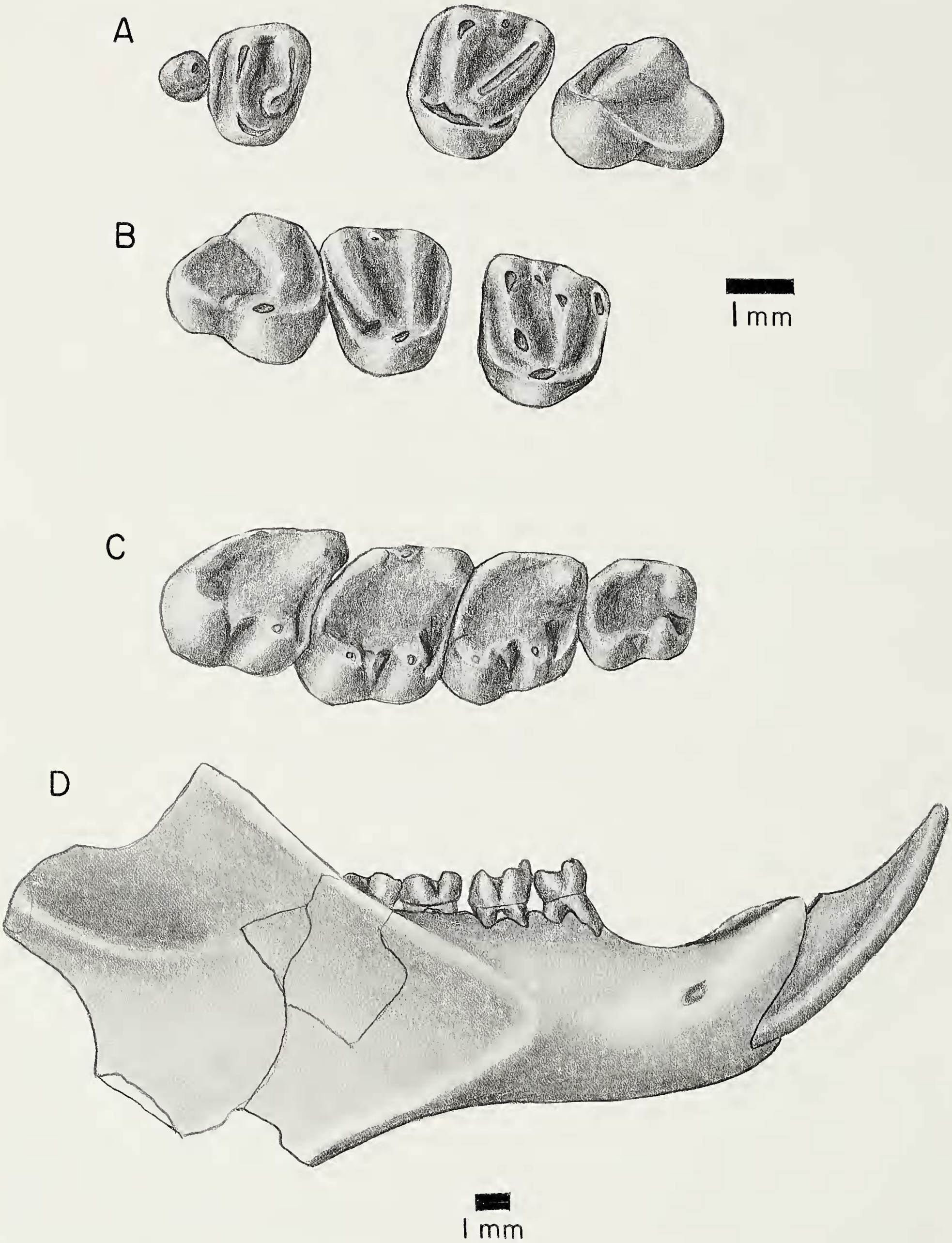

Fig. 5.—Mandible and dentitions of *Spermophilus* (*Otospermophilus*) *jerae*. A, left P^3–P^4, M^2–M^3, CM 27834 (holotype). B, right M^1–M^3, CM 27835. C–D, CM 27836. C, right P_4–M_3. D, lateral view of mandible.

Table 5.—*Dental measurements of* Speromphilus (Otospermophilus) jerae. *Measurements in mm. Abbreviations as in Table 2. Additional abbreviations: L, left; R, right.*

		P^3		P^4		M^1		M^2		M^3	
		a-p	tr	a-p	tr	a-p	tr	a-p	tr	a-p	tr
CM 27834	L	0.60	0.71	1.50	1.82	—	—	1.92	2.26	2.27	2.17
	R	0.06	0.71	1.45	1.84						
CM 27835						1.78	2.10	1.92	2.21	2.22	2.11

	P_4		M_1		M_2		M_3	
	a-p	tr	a-p	tr	a-p	tr	a-p	tr
CM 27836	1.62	1.64	1.90	2.20	2.11	2.26	2.32	2.15
CM 27838	1.54	1.52	—	—	2.06	2.20	2.26	2.25
CM 27839	1.42	1.50	1.62	1.81	1.75	2.12	2.12	2.08
CM 27840	—	—	1.82	2.17	2.62	2.28	2.23	2.19

rated only by a narrow slit. There is no sign of a metalophid closing the trigonid basin. The buccal valley is narrow and shallow, being blocked internally by a low ectolophid. The posterolophid is low and arcs gently anteriorly to end in a small but distinct entoconid. A small mesostylid is present.

M_1 is slightly compressed anteriorly and has a high metaconid. The anterior cingulum is short, ending in an anteroconid near the base of the protoconid. The short metalophid is complete, isolating a small, lingually displaced trigonid basin. The buccal valley is short, shallow, and blocked by a poorly defined mesoconid. The posterolophid forms a smooth arc from the hypoconid to the entoconid, which is almost completely submerged in the posterolophid. There is only the slightest hint of a mesostylid on the lingual border of the tooth.

M_2 is similar to M_1 but is more anteroposteriorly compressed. On CM 27836 the trigonid is open, with the metalophid trailing off into the talonid basin, not making contact with the metaconid, and there is a better developed mesostylid. The rest of the specimens all have closed trigonids and poorly developed mesostylids as on M_1.

M_3 has an open trigonid or slightly closed trigonid and is similar anteriorly to the anterior molars. Posteriorly, the tooth does not show anteroposterior compression but has an inflated posterolophid, especially in the region of the hypoconid. The posterolophid terminates in an entoconid which is not completely submerged into the lophid except in CM 27836 in which the entoconid region is indistinct. Also in CM 27836, the width of the talonid basin is narrower than in other specimens.

Some postcranial material was recovered in association with the skulls and mandibles (CM 27844); however, most of it is shattered or incomplete. A partially articulated rear foot and associated astragalus indicate that, in general, the foot was comparable to that of the Recent *S.* (*Otospermophilus*) *varigatus.* Other postcranial elements, such as the proximal part of a femur and ulna, agree in structure, but are smaller than in *S. varigatus.*

Discussion.—Of the Tertiary spermophiles that have been described, *Spermophilus jerae* is most similar to *S. tephrus* from the late Hemingfordian of Oregon (Gazin, 1932) and *S. primitivus* from the Barstovian of Montana (Bryant, 1945). *Spermophilus tephrus,* known from three skulls and no mandibular material, seems to provide a reasonable ancestral condition. *Spermophilus jerae* differs from *S. tephrus* in having a reduced mesostyle on the upper molars and an elevated parastyle. Black (1963) stated that *S. primitivus* was probably descended from *S. tephrus* with modifications in the zygomatic plate and parastyles of the upper cheek teeth. *Spermophilus jerae* resembles *S. primitivus* in the high parastyles but not in the large mesostyles and, in the mandible, the heavy development of the masseteric crests. If *S. primitivus* and *S. jerae* are derived from a *S. tephrus*-like condition, they have developed along different morphological paths, with *S. jerae* being a smaller, lightly muscled form, and *S. primitivus* being larger with a heavier masseteric complex. Both forms are primitive in the extent of the masseteric fossa, which extends only to below M_1 and not forward to the P_4 as in most Barstovian to Recent species.

Genus *Cynomys* Rafinesque, 1817

?*Cynomys* sp. indet.

(Fig. 2)

Referred Specimens.—CM 27842, left mandible fragment with M_3; CM 27843, left P3.

Measurements.—CM 27842, M_3: a-p, 3.53 mm; tra, 2.74 mm; trp, 2.16 mm. CM 27843, P^3: a-p, 1.87 mm; tr, 2.08 mm.

Description.—The upper premolar (CM 27843) differs little in structure from that of advanced marmotines except in size and crown height. The tooth is round in occlusal outline and has a high central transverse crest flanked anteriorly and posteriorly by shelves emarginated by cingula. The anterior shelf is short and slopes lingually, while the posterior shelf is widest at the midpoint of the tooth and also slopes lingually.

M_3 is elongate, and the trigonid is high, closed anteriorly and posteriorly, and strongly compressed anteroposteriorly. The metalophid is complete, extending from the protoconid to the base of the metaconid. The trigonid basin is also compressed, pit-like, and close to the protoconid. The buccal valley is moderately deep but short, with a prominent mesoconid on the short ectolophid blocking the valley lingually. The talonid basin is deep and rugose, resulting from a crest-like structure originating at the mesostylid and extending to the mesoconid, and anterolingually from there to submerge into the floor of the basin. The posterolophid is moderately high and inflated with only a slight thinning between the entoconid and the hypoconid. The posterolophid is heavier than in living spermophiles, and the posterior segment of the basin is laterally compressed, resulting in a narrower talonid basin than in most spermophiles. The entoconid is separated from the mesostylid by a shallow notch, and the lingual margin of the tooth extends uninterrupted from the mesostylid to the metaconid. The talonid basin is, therefore, completely closed. The floor of the talonid basin has several deep pits.

Discussion.—The two specimens questionably referred here to *Cynomys* differ from the same cheek teeth of Recent *C. ludovicianus* in being smaller and slightly lower crowned. No species of *Spermophilus* has the accessory lophid in the talonid basin of M_3 that is shared by the Anceney specimen and *Cynomys.* P^3 from Anceney, CM 27843, is more lophate than that of any species of *Spermophilus,* and the anterior cingulum is also much better developed in CM 27843.

Previously, the earliest occurrence of *Cynomys* in the fossil record was from the late Blancan (Hibbard, 1942; Eshelman, 1975), leading to speculation that it evolved rather rapidly from spermophiles (Black, 1963). However, if these Anceney specimens are on the evolutionary line leading to *Cynomys,* future collections should reveal intermediate species and substantiate this occurrence.

Family Castoridae Gray, 1821

Genus *Euroxenomys* Samson and Radulesco, 1973

Discussion.—*Euroxenomys* was named by Samson and Radulesco (1973) for the species *Chalicomys minutus* Meyer (1838) from the Miocene (Astracian) of Europe. It was diagnosed as a small beaver with: anteriorly convex incisors; mesodont, rooted cheek teeth; premolars larger than molars; P^4 with deep parastria and hypostria; P_4 with only one lingual striid (mesostriid); M^3 longer than M^2; and three open flexids on the lower molars. They distinguished this genus from *Monosaulax* by the persistent parastria on P^4 and elongate M^3.

Euroxenomys minutus was viewed as a primitive member of the lineage that possibly led to the Plio–Pleistocene Eurasian *Trogontherium* (Samson and Radulesco, 1973). Savage and Russell (1983) listed this species as *Trogontherium minutus.* However, the much larger size, greater hypsodonty of the cheek teeth, greater complexity of the occlusal pattern of the molars, and unique morphology

Table 6.—*Dental measurements of* Euroxenomys inconnexus. *Measurements in mm. Abbreviations as in Table 2.*

		n	$\bar{x}$	or	s	cv
P^4	a-p	1	3.25	—	—	—
	tr	1	3.22	—	—	—
M^1	a-p	7	2.91	2.35–3.20	0.27	9.44
	tr	7	2.96	2.51–3.25	0.29	9.94
M^2	a-p	2	2.83	2.80–2.85	—	—
	tr	2	2.98	2.97–3.00	—	—
M^3	a-p	2	2.65	2.60–2.70	—	—
	tr	2	2.70	2.55–2.85	—	—
P_4	a-p	1	4.60	—	—	—
	tr	1	3.50	—	—	—
M_1	a-p	4	2.80	2.45–3.00	0.21	7.52
	tr	5	3.30	2.63–3.63	0.35	10.73

of the incisors of *Trogontherium* clearly distinguish it from *Euroxenomys.* Both of these genera share the derived feature of an elongate M^3, however, which may indicate a close relationship.

Euroxenomys inconnexus, **new species**
(Fig. 4, Table 6)

Monosaulax pansus? (Cope) Dorr, 1956.

Holotype.—CM 8925, partial skull with incisors and right P^4–M^3 and right mandible with I_1, P_4–M_1.

Horizon and Locality.—Anceney local fauna, center N 1/2, sec. 13, T2S, R3E, Madison Valley Formation, Gallatin County, Montana.

Age.—Early Barstovian (middle Miocene).

Referred Specimens.—CM 28558–28563, KU 40354–40355, isolated upper molars; CM 10878, 28564–28566, isolated lower molars; CM 10869, incisors.

Diagnosis.—Differs from the type species, *E. minutus* in being smaller and having the mesoflexid on lower molars remain open until moderately worn (remains open longer on type species).

Etymology.—Latin, *inconnexus,* separate or unjoined.

Description.—CM 8925 consists of a crushed partial skull and partial right mandible. The braincase is missing from the specimen and the premaxillary–nasal area of the skull is badly distorted. The upper incisors are preserved and are anteriorly convex in cross section as is typical for *Monosaulax.* The diastema appears to be highly arched and reasonably short. The zygomatic plate is fairly large and is preserved only on the left side of the skull. The orbital areas are not preserved well enough for description. The palatine area has two posterior palatine foramina at the level of M^2 with the suture just anterior to them. The mandible is broken behind M_2 and below P_4, but the diastema is intact and not sharply recurved but elongate. The mental foramen is below and anterior to the roots of P_4 and is rounded in outline. The teeth are relatively high crowned and rooted with very little cement visible.

P^4 is the largest upper cheek tooth and is characterized by a deep hypostria extending to the base of the crown. Anteroexternally, the parastria also is very long, extending to the base of the enamel on the erupting tooth. The parastria is deep but not as deep as the hypostria. There is also a very shallow mesostria which will close in very early wear stages. The paraflexus remains open until very late wear, but the mesoflexus will close very early. Behind the mesoflexus is a small metafossette which does not open to form a flexus at any point.

M^1 and M^2 are extremely similar and cannot be distinguished from one another when isolated. In all specimens recovered, the parafossette and metafossette are closed. The parafossette abuts the hypoflexus and the mesofossette arcs posteriorly to terminate on or near the posterior border of the tooth. The metafossette is in the posterolabial corner of the tooth. Both M^1 and M^2 taper toward the base of the crown.

M^3 is similar to the first two molars and is rounded along its posterior border, with the metafossette being central rather than posterolabial. The mesofossette terminates posterolingually rather than centrally, and the parafossette abuts the hypoflexus as in the other molars. Unlike the anterior molars, M^3 widens toward the base of the crown instead of tapering.

In CM 8925, P_4 is unworn and has a deep hypoflexid extending to the base of the tooth and a mesoflexid which extends about 3/4 of the total height of the crown. The parafossettid is completely enclosed and connected to the metafossettid by a thin central mure. The metafossettid is also enclosed but, in the unworn state, is divided by a very thin enamel ridge into two fossettids. This condition is presumably lost very early in wear.

On M_1 and M_2 the deep hypoflexid and mesoflexid do not abut as they do in P_4, but rather the mesoflexid passes anteriorly to the posteriorly directed hypoflexid. The hypoflexid abuts the posterolingual metafossettid while the parafossettid contacts the lingual margin of the tooth and arcs anteriorly to the midpoint of the anterior margin.

Discussion.—The Anceney castorid is referable to the otherwise Eurasian genus *Euroxenomys* based on the deep parastria of P^4, simple P_4 (only mesostriid on lingual side), small size, mesodont cheek teeth, and anteriorly convex incisors. *Euroxenomys* was also diagnosed as having M^3 longer (anteroposteriorly) than M^2 (Samson and Radulesco, 1973). The anteroposterior occlusal measurement of M^3 in the holotype of *E. inconnexus* is less than that of M^2 (Table 6). However, CM 8925 is a young individual (permanent premolars just coming into occlusion). Due to the tapering of M^2 and the widening of M^3 toward the bases of the crowns of these teeth, it is evident in labial view that after only a moderate amount of wear, M^3 will be longer than M^2. The anteroposterior measurements of M^2 taken 1 mm above the present occlusal surface on the labial side is 2.1 mm. On M^3 this measurement is 2.7 mm. Clearly, M^3 is longer than M^2 in *E. inconnexus* except in early stages of wear. *Euroxenomys inconnexus* differs from the European type species in being smaller.

Although similar in size, *E. inconnexus* differs from *Monsaulax curtus* from the early Barstovian Olcott Formation of Sioux County, Nebraska (Matthew and Cook, 1909), in the greater depth of the parastria on P^4 and elongation of M^3. Two specimens containing upper dentitions from the Olcott Formation are present in the collections of the American Museum of Natural History (FAM 64839 and FAM 64840). Both are equivalent in size to the type mandible of *M. curtus* and the cheek teeth are of the same crown height. These specimens lack labial striae on the upper premolars unlike P^4s of *Euroxenomys*. The M^3s of referred specimens of *M. curtus* are also not elongated as in *E. inconnexus* and the European type species. The Anceney species, however, has a P_4 with only one lingual striid (mesostriid) and thus fits part of the diagnosis of *Monosaulax* (Stirton, 1935).

Structurally, the Anceney species resembles the older Hemingfordian Martin Canyon Quarry A material from northeastern Colorado, first described by Galbreath (1953) as *Monosaulax* nr. *M. curtus* and discussed at length by Wilson (1960). Wilson referred this material to *Monosaulax* n. sp. *Euroxenomys inconnexus* is more advanced than the Colorado species in its greater crown height and length of hypostria on the upper cheek teeth. M^3 of the Colorado species is longer than M^2, diagnostic of *Euroxenomys*. This suggests the possibility that the Anceney species may be derived from a species very similar to "*Monosaulax* n. sp.," and that it is also referable to *Euroxenomys*. The occurrence of an otherwise

European genus from the Quarry A fauna is consistent with the remainder of the fauna in that several other European genera have been cited (Wilson, 1960).

Family Heteromyidae Gray, 1868
Subfamily Heteromyinae Gray, 1868
Genus *Mookomys* Wood, 1931
Mookomys thrinax, **new species**
(Fig. 6, Table 7)

Holotype.—CM 28502, left mandible with I_1 and P_4–M_2.

Horizon and Locality.—Anceney local fauna, center N 1/2, sec. 13, T2S, R3E, Madison Valley Formation, Gallatin County, Montana.

Age.—Early Barstovian (middle Miocene).

Referred Specimens.—CM 27987, 27991, 27995, 38509, 28576, 28577, KU 28562, maxillae with upper cheek teeth; CM 28005, 28019, 28021, 28038, 28050, 28056, 28074, 28076, 28079, 28080, 28083, 28089–28091, 28097, 28100, 28129, 28140, KU 28548, 28569, 28582, 28609, 28613, 28651, isolated P^4s; CM 28023, 28373, 28382–28386, 28429, 28434, 28445, 28449, 28452, 28453, 28456, 28495, 28497, 28499, KU 28579, 28674, isolated upper molars; CM 28508, 28515, 28516, 28517, mandibles with cheek teeth; CM 28310, 28338, 28340, 28342, 28476, KU 28685, isolated P_4s; CM 28251, 28253, 28283, 28480, 28485, 28489, 28493, 28494, isolated lower molars; CM 40860, six isolated upper incisors.

Diagnosis.—Differs from the type species, *M. altifluminis* in having hypolophid cusps of P_4 anteroposteriorly compressed, and cheek teeth slightly higher crowned; differs from all known heteromyids by the morphology of the anterior cingulum of M^1 (cingulum extends extends anteriorly from paracone, then lingually, isolating the protocone).

Etymology.—Greek, *thrinax*, three-pronged fork, intended to refer to Three Forks Basin, Montana.

Description.—The upper incisors referred to *M. thrinax* are narrow (buccolingually) with a gently convex anterior enamel surface and a distinct, narrow, but deep central groove.

The cheek teeth are mesodont. P^4 has an isolated oval protocone on the protoloph. A minute paracone occurs in some specimens on the buccal slope of the protocone. The metaloph is typically three-cusped with the hypostyle only slightly anterior to the other cusps. Unlike most heteromyines, the union of the protocone to the metaloph is just lingual to the center of the metaloph, as in the premolars of perognathines.

The upper molars are typically bilophate, with three cusps on each loph. The lingual cusps (hypostyle and protostyle) are the smallest, the buccal cusps (paracone and metacone) are anteroposteriorly compressed, and the central cusps (hypocone and protocone) are the largest. The protoloph is wider than the metaloph (buccolingually) on the upper molars, and M^1 is larger than M^2. A unique feature of M^1 is the configuration of the anterior cingulum. It arises from the lingual end of the paracone, is directed anteriorly, then bends lingually, fusing to the buccal side of the protostyle. This isolates the protocone from the anterior cingulum and creates a small enamel lake between the anterior cingulum and the protocone. There is no evidence of a posterior cingulum on the upper molars. The anterior cingulum on M^2 is reduced to a small anterior bulge at the anterolingual corner of the paracone. In all other features, M^2 resembles M^1. M^3 is unknown.

The mandible is slender with a flat ventral border. The masseteric scar extends well anterior to the tooth row, relatively high on the side of the mandible and is ventrally continuous with a ridge, marking the attachment of the masseter. The mental foramen is anterior and ventral to the masseteric ridge. The diastema is shallow.

The lower incisor is laterally compressed, as is I^1, and the anterior enamel surface has a narrow, flat central part, but is otherwise convex.

The metalophid of P_4 is narrower (buccolingually) than the hypolophid and consists of only two subequal cusps (metaconid and protostylid). A distinct valley separates the metalophid cusps, and a transverse valley separates the metalophid from the hypolophid. The hypolophid also consists of only two cusps (hypoconid, entoconid). The cusps of the hypolophid are, however, anteroposteriorly compressed making them buccolingually elongate. There is no indication of accessory cusps on the referred

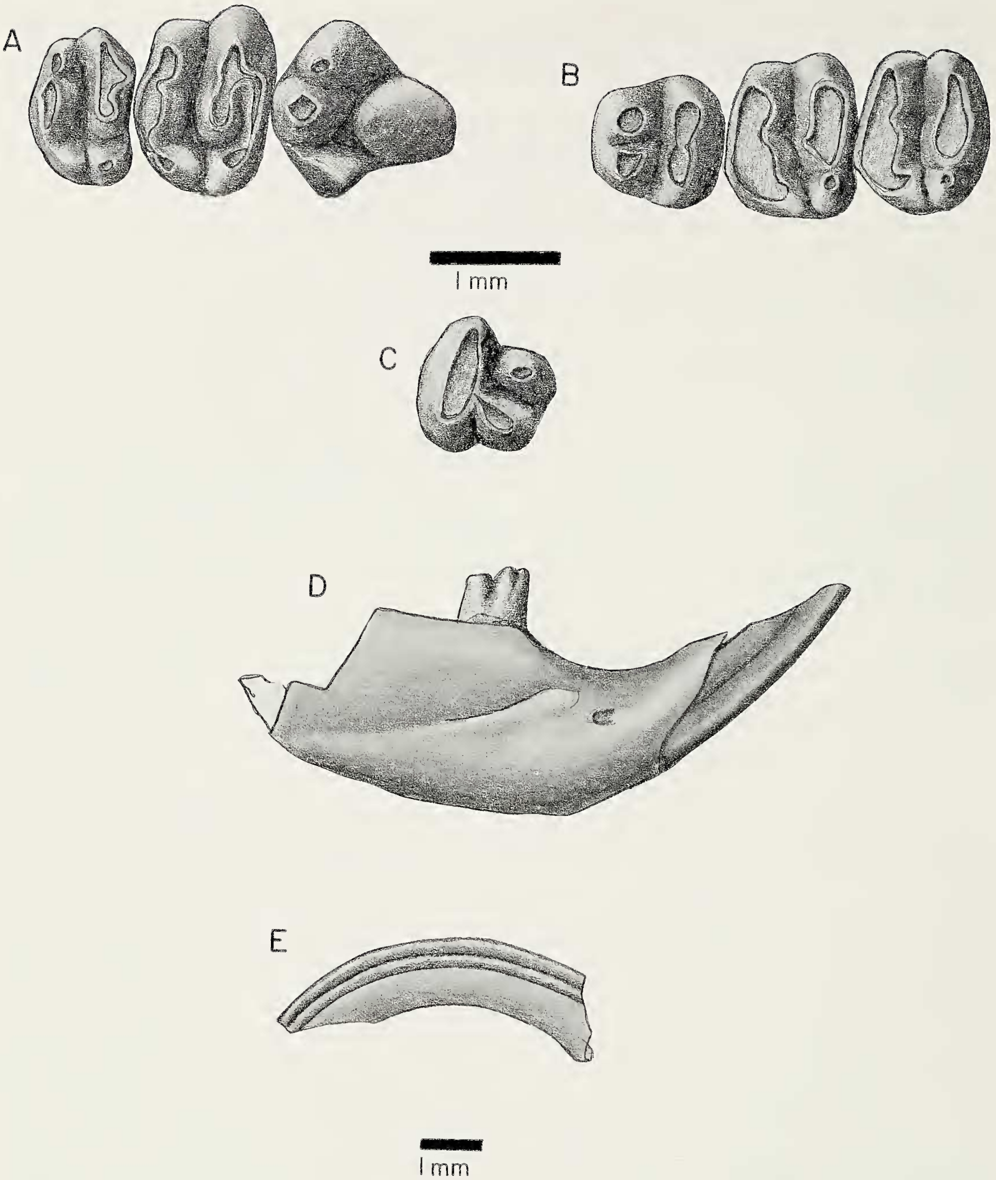

Fig. 6.—Mandible and dentitions of species of *Mookomys thrinax.* A, right P^4–M^2, CM 28576. B, left P_4–M_2, CM 28502 (holotype). C–D, CM 28517. C, right P_4. D, lateral view of mandible. E, lateral view of left I^1, CM 40860.

lower premolars. The metalophid appears to unite lingually with the hypolophid after wear (metaconid to hypoconid) as in *M. altifluminis.*

The molars are wider than P_4 and consist of two rows of three cusps each. A short anterior cingulum is anterior to the protoconid and continuous with the protostylid. After only moderate wear, it fuses with the protoconid and the remainder of the metalophid. With wear the lophs of the molars unite either centrally or buccally. M_3 is the smallest of the molars and differs from the anterior molars only in having a narrower (buccolingually) hypolophid that has more anteroposteriorly compressed cusps.

Table 7.—*Dental measurements of* Mookomys thrinax. *Measurements in mm. Abbreviations as in Tables 2 and 5.*

		n	$\bar{x}$	or	s	cv
P^4	a-p	28	1.24	1.04–1.41	0.09	7.26
	tra	28	0.61	0.47–0.77	0.07	10.98
	trp	28	1.27	1.09–1.44	0.07	5.43
M^1	a-p	21	0.97	0.87–1.10	0.05	5.46
	tra	21	1.32	1.18–1.43	0.07	5.23
	trp	21	1.26	1.14–1.38	0.06	5.08
M^2	a-p	4	0.88	0.82–1.00	0.08	9.66
	tra	4	1.18	1.11–1.23	0.05	4.58
	trp	4	1.05	0.99–1.09	0.04	4.00
P_4	a-p	7	1.01	0.93–1.09	0.06	5.94
	tra	7	0.76	0.70–0.82	0.04	5.53
	trp	7	0.92	0.85–1.00	0.06	6.20
M_1	a-p	8	1.01	0.96–1.10	0.04	4.06
	tra	8	1.18	1.10–1.25	0.05	4.41
	trp	8	1.18	1.13–1.21	0.04	3.05
M_2	a-p	3	1.02	1.00–1.07	0.04	3.92
	tra	3	1.17	1.13–1.20	0.04	3.25
	trp	3	1.13	1.09–1.19	0.05	4.69
M_3	a-p	1	0.91			
	tra	1	0.98			
	trp	1	0.90			

Discussion.—This species is clearly referable to *Mookomys* as diagnosed by Wood (1931) because of its simple four-cusped P_4, similar crown height of the cheek teeth, and sulcate upper incisor. No upper incisors were found in association with the cheek teeth referred to *M. thrinax,* but among the fauna from Anceney, only one other rodent (of similar size) is known to have grooved incisors, *Perognathus. Perognathus* is quite rare in the Anceney fauna (fewer than 19 specimens) while *M. thrinax* is the second most abundant heteromyid, represented by more than 70 specimens. Therefore, the assignment of the isolated incisors to the latter is far more likely than to *Perognathus.*

Mookomys thrinax differs from the type species of the genus only in its slightly higher crowned cheek teeth and in having more anteroposteriorly compressed cusps on P_4.

"*Mookomys*" cf. "*M.*" *formicarum* Wood, 1935
(Fig. 9F)

Referred Specimens.—CM 28496, CM 28500, isolated M^1's.

Measurements.—CM 28496: a-p, 0.96 mm; tra, 1.28 mm; trp, 1.24 mm. CM 28500: a-p, 0.93 mm; tra, 1.26 mm; trp, 1.18 mm.

Description.—M^1 is low crowned with six cusps inflated and completely separate from one another to their bases, with the exception of the hypostyle and protostyle, which are only slightly joined to the hypocone and protocone respectively. There is no evidence of either an anterior or a posterior cingulum connecting the cusps. The central transverse valley is shallow lingually, deep labially, and straight, paralleling the protoloph. The metaloph is slightly convex, with the hypocone being the most posterior cusp. The crown of the tooth is inflated basally, under which are three well-developed and strongly separated roots.

Discussion.—The two teeth representing this taxon could not be associated with any other teeth in the fauna. Since they are distinct in morphology, it is unlikely that other aspects of the dentition have gone unnoticed. The Anceney material corresponds to what has been called *Mookomys formicarum* from the Arikareean of Nebraska, but is slightly larger (Wood, 1935:table II). This material is also comparable to that described as *Mookomys* cf. *M. formicarum* from the Barstovian of California, and there is little difference in comparable dental elements (Lindsay, 1972). In the original description of *M. formicarum,* Wood (1935:fig. 8b) designated CM 10177 as the type and identified it as an M_1. However, it is more likely an M^1 (Lindsay, 1972). Since at least the mid-1950s, the holotype of *M. formicarum* has been lost (Reeder, 1956), complicating matters even more.

It is questionable whether *M. formicarum* should be referred to *Mookomys.* The cheek teeth referred here and elsewhere to *M. formicarum* differ from the type species of the genus in both crown height and degree of lophodonty. Reeder (1956) first noted the difference in crown height of this species from that of the genotypic species *M. altifluminis* from the Hemingfordian of Montana. Because of this difference he referred *M. formicarum* to *Perognathus.* However, on all the reported specimens of *M. formicarum* the cusps of the teeth are entirely isolated from one another and no semblance of a loph exists. The cheek teeth of all species of *Perognathus* have distinct lophs developed. Similarly, on the holotype of *M. altifluminis* as well as the material of the referred species (described above), the major transverse lophs of the molars are clearly distinguishable, unlike the teeth referred to *M. formicarum.* It is evident that *M. formicarum* belongs in a heteromyid genus other than *Mookomys.* However, the peculiar lack of lophodonty and cingula on the molars of *M. formicarum* are unknown among other recognized heteromyids. It is possible that *M. formicarum* should be included in a new genus of heteromyid, but it is so poorly known that naming such a new genus would be inappropriate at this time. Therefore, this species is included in *Mookomys* here only as a matter of convenience.

Wood (1935), in naming *Mookomys "formicorum,"* incorrectly applied the masculine or neuter Latin ending to his species name. The correct form of the trivial name with the feminine ending should be *formicarum* (Reeder, 1956:135).

Genus *Peridiomys* Matthew, 1924

Peridiomys sp.

(Fig. 7)

Referred Specimen.—CM 27876, left mandible with incisor and P_4–M_3.

Measurements.—P_4: a-p, 1.37 mm; tra, 1.10 mm; trp, 1.30 mm. M_1: a-p, 1.22 mm; tra, 1.48 mm; trp, 1.48 mm. M_2: a-p, 1.17 mm; tra, 1.40 mm; trp 1.36 mm. M_3: a-p, 1.06 mm; tra, 1.18 mm; trp, 1.07 mm.

Description.—The mandible is not flat ventrally but curves gently from the angular process to the diastema, where it turns sharply dorsally. The body of the ramus is heavy and deep, appearing almost geomyid-like. The diastema is sharply recurved and ends in the incisive alveolus above the level of the molariform teeth. Laterally, the surface is smooth except for the well-developed masseteric crest beginning below M_2 near the base of the jaw, and extending dorsally in a straight line to end just anterior to P_4 above middepth of the diastema. The mental foramen is anterior to and slightly below the terminus of the masseteric crest at middepth of the jaw. Posteriorly, the ascending ramus arises at the anterior margin of M_2, but its full extent cannot be seen due to breakage. The incisor capsule is

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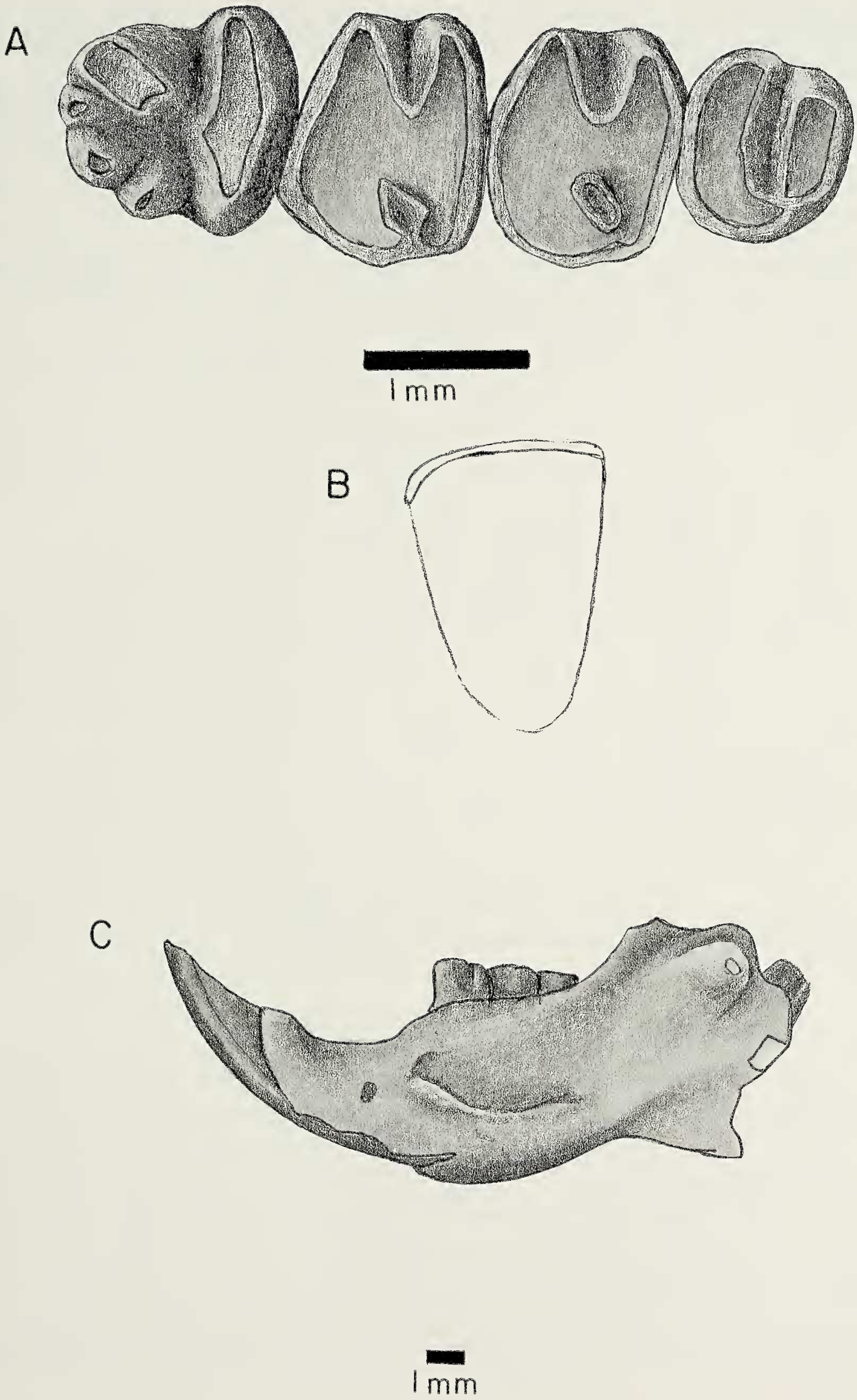
Fig. 7.—*Peridiomys* sp., CM 27876. A, Occlusal view of left P_4–M^3. B, Cross section of left I_1 (anterior to top, lateral side to left). C, Lateral view of mandible.


A
1mm
B
C
1mm

preserved and obvious as an inflated area on the lateral side of the ascending ramus. Ventrally, only a small part of the angular process remains and, judging from the small amount preserved, appears to have been sharply inflected.

The lower incisor is heavy and flattened anteriorly. The metalophid of P_4 is composed of four cusps. Labially, a small, rounded protostylid is discernible. Lingually, a much larger and more anterior metaconid is present. Along the anterior margin of the tooth are two smaller anterostylids that form a continuous, anteriorly convex loph between the protostylid and metaconid that preserves a shallow trigonid basin. The central transverse valley of the tooth is shallowest at its center, from which it slopes labially and lingually. The lingual opening of the valley is deeper and wider than the labial. The hypolophid is worn, with all cusps conjoined to form a straight lophid.

The lower molars are all well worn, with M_1 and M_2 similar in size and configuration, and M_3 only slightly smaller. The remaining pattern indicates that the protostylid was elongate and the transverse valley was deflected posteriorly. As wear proceeded the metalophid and hypolophid joined across the stylids, centrally isolating a small, persistent pit between the two points of union. The teeth are only moderately high crowned but very heavily rooted.

In occlusal view, M_3 is almost rounded and union of the metalophid and hypolophid occurred labially and progressed lingually. There is no evidence of a pit developing between the stylids and the center of the tooth as in the anterior molars.

Discussion.—This specimen is clearly referable to *Peridiomys* because the lower incisor is broad and flattened anteriorly, the cheek teeth are moderately low crowned, the metaconid of P_4 is markedly larger than the protostylid, and P_4 preserves the characteristic heteromyine central enamel pit.

The greatest difference between *Peridiomys* sp. and the type species, *P. rusticus* Matthew (1924), is its much smaller size. P_4 of *Peridiomys* sp. has multiple anterostylids and is longer (anteroposteriorly) than wide. In the type species, P_4 is wider than long and there are no accessory cuspules on the metalophid (Matthew, 1924; Wood, 1935). *Peridiomys* sp. differs from *P. oregonensis* again in being smaller, having a broader lower incisor, and having the metaconid of P_4 much larger than the protostylid. These cusps are subequal in size in *P. oregonensis* and *P. borealis* (Gazin, 1932; Wood, 1935; Storer, 1970, 1975).

It is possible that this specimen, CM 27876, belongs to *Peridiomys halis* (described below). However, it is about 11% smaller than the smallest specimen of *P. halis* and nearly 25% smaller than the mean measurements of *P. halis* (Table 8). The metalophid of P_4 of *Peridiomys* sp. is also relatively broader than those of *P. halis.* The specimen referred here to *Peridiomys* sp. may represent a new, small species of *Peridiomys.* However, no new name will be proposed until additional material is collected, and its differences from *P. halis* can be shown to be consistent.

Peridiomys halis, **new species**

(Fig. 8, Table 8)

Holotype.—CM 40861; partial skull with incisors and left P^4–M^2, associated mandible with incisor and right P_4–M_3, and partial postcranial skeleton.

Referred Specimens.—CM 27869–27870, 27873, 27874, 27877, KU 28472–28473, partial maxillae with cheek teeth; CM 27879–27891, KU 28476, dP^4; CM 27872, 27878, 27882–27884, 27887–27895, KU 28471, 28474, 28477–28487, P^4; CM 27898–27908, 27910, KU 28469–28470, 28475, 28488–28495, M^1; CM 27911–27916, 27918–27921, KU 28496, 28498–284503, M^2; CM 27922–27925, 27927–27928, KU 28504, 28506–28508, M^3; CM 27930–27934, KU 28509–28514, M^1 or M^2; CM 40857, partial mandible with P_4–M_1; CM 27948–27950, dP_4; CM 27935–27939, 27941, 27944–27947, 40858, KU 28515–28521, P_4; CM 27868, 27951–27958, KU 28522–28527, M_1; CM 27959–27969, KU 28528–28535, M_2; CM 27970–27974, KU 28536–28540, M_3, CM 27975–27978, M_1 or M_2.

Horizon and Locality.—Anceney local fauna, center N 1/2, sec. 13, T2S, R3E, Madison Valley Formation, Gallatin County, Montana.

Table 8.—*Dental measurements of* Peridiomys halis. *Measurements in mm. Abbreviations as in Tables 2 and 5.*

		n	$\bar{x}$	or	s	cv
dP^4	a-p	3	2.03	2.00–2.90	0.05	—
	tr	3	1.99	1.90–2.08	0.09	—
P^4	a-p	30	2.11	1.82–2.32	0.13	5.99
	tra	31	1.14	0.93–1.32	0.10	8.54
	trp	31	2.12	1.92–2.30	0.01	5.81
M^1	a-p	27	1.57	1.39–1.72	0.10	6.34
	tra	26	2.11	1.85–2.34	0.14	6.68
	trp	26	1.98	1.67–2.25	0.15	7.40
M^2	a-p	19	1.47	1.20–1.64	0.13	8.94
	tra	19	1.92	1.71–2.23	0.13	6.94
	trp	19	1.76	1.58–1.94	0.12	6.57
M^3	a-p	11	1.27	1.09–1.28	0.12	9.49
	tr	11	1.44	1.44–1.63	0.12	8.07
dP_4	a-p	2	2.05	2.00–2.10	—	—
	tr	2	1.34	1.28–1.48	—	—
P_4	a-p	19	1.84	1.64–2.03	0.12	6.40
	tra	19	1.39	1.03–1.63	0.13	9.45
	trp	19	1.64	1.28–1.81	0.12	7.37
M_1	a-p	17	1.58	1.39–1.73	0.11	6.70
	tra	17	1.94	1.75–2.20	0.15	7.82
	trp	18	1.91	1.68–2.20	0.16	8.27
M_2	a-p	21	1.50	1.33–1.67	0.11	7.61
	tra	21	1.94	1.61–2.12	0.12	6.17
	trp	21	1.81	1.54–1.96	0.14	7.52
M_3	a-p	12	1.34	1.20–1.45	0.07	5.54
	tra	12	1.58	1.41–1.67	0.07	4.52
	trp	12	1.31	1.18–1.47	0.08	5.89

Age.—Early Barstovian (middle Miocene).

Diagnosis.—Differs from type species, *P. rusticus* in having P_4 longer than wide with at least one large anterostylid, and central protoconid variably present on P_4. Differs from all other species of the genus in its larger size.

Etymology.—Greek, *halis,* in abundance.

Description.—Only the rostrum and part of the palate are preserved in the skull of the holotype. The rostrum is long, dorsoventrally deep, and transversely narrow. The diastema is long (9.6 mm) and essentially flat ventrally with a slight ventral curve at the anterior end just behind the incisors. Two shallow, parallel grooves are preserved on the palate beginning at the incisive foramina and running posteriorly. The incisive foramina are small, about 35% of the length of the diastema. The premaxillary–maxillary suture crosses the palate at the posterior ends of the incisive foramina. The infraorbital foramen is accompanied by a larger anterior rostral perforation that is just ventral to middepth of the rostrum, dorsal to the incisive foramen. A small bony bulge is ventral to the infraorbital foramen. No other features of the skull are discernible due to breakage and poor preservation.

The upper incisors are broad and asulcate. The anterior enamel surface is only slightly convex and nearly flattened.

DP^4 is triangular and has three rows of cusps. The anterocone is single or slightly doubled and forms the anterior margin of the tooth. The protocone is central and is connected to the smaller paracone by a short crest. These cusps become joined early in wear. Forming the posterior margin of the tooth is the large hypocone. A large hypostyle joins the hypocone posteriorly and is taller than the remainder of the cusps. The hypostyle is directed anteroposteriorly and extends to the anterocone.

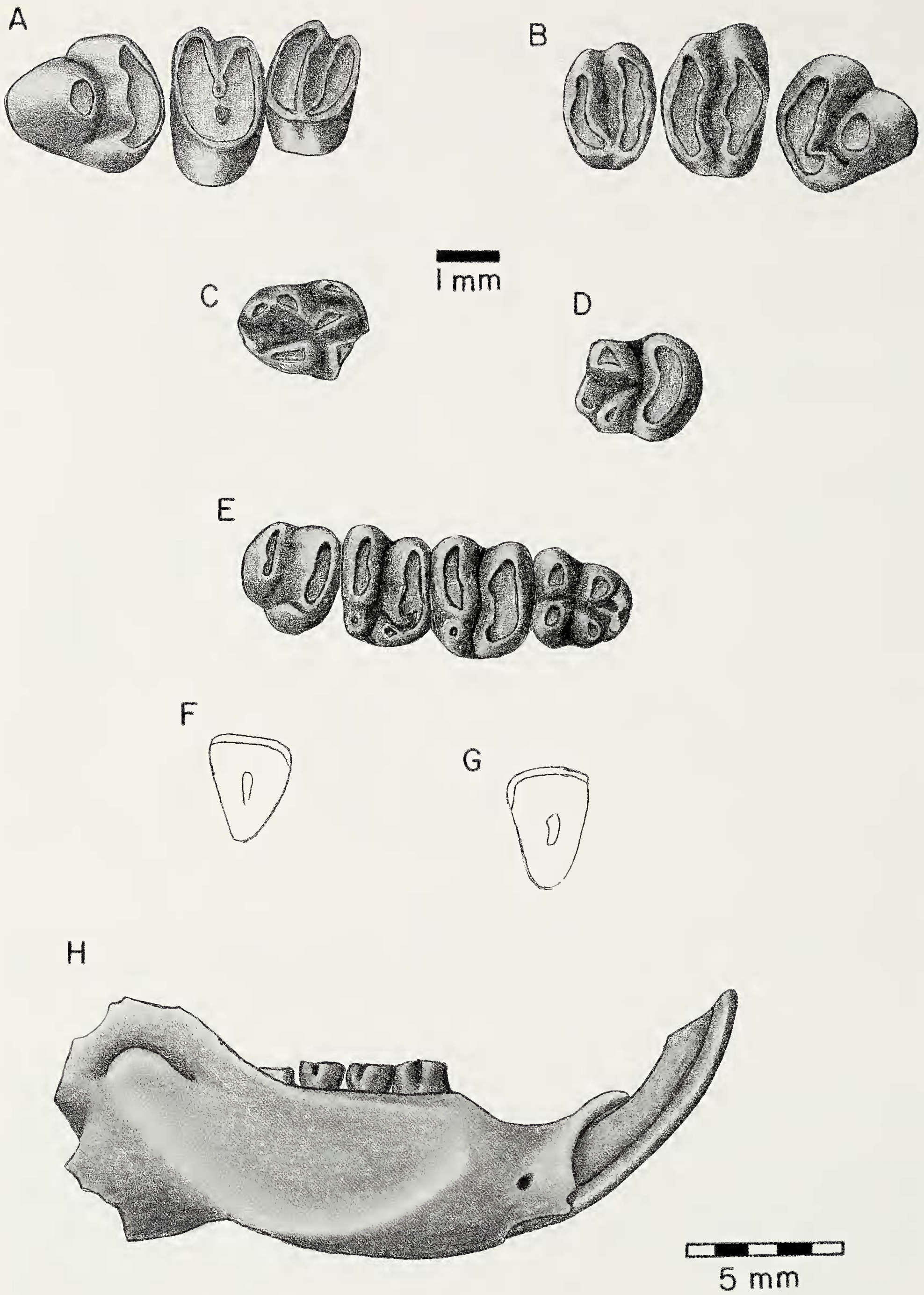


Fig. 8.—Mandible and dentiton of *Peridiomys halis.* A, left P^4–M^2, CM 40861 (holotype). B, right P^4–M^2, CM 27870. C, right dP_4 (broken), CM 27949. D, left P_4, CM 40858. E–H, CM 40861 (holotype). E, right P_4–M_3. F, right I_1 (anterior to top). G, right I^1 (anterior to top). H, Lateral view of mandible.

P^4 is triangular in occlusal outline and is about as wide as long. It is moderately high crowned and has three distinct roots. The protocone is slightly oval, wider than long, and usually unites with wear to the lingual margin of the hypocone or to the hypostyle. The protocone may have an accessory cuspule either anterolingually or labially. In two specimens (KU 28479 and KU 28482) the labial cuspule is large and distinct, giving the protoloph an appearance of being almost as wide as the metaloph. In most specimens, the transverse valley is highest between the hypocone and protocone, falling off steeply from that point both labially and lingually. The metaloph is composed of the hypostyle, hypocone, and metacone, the largest of which is the central hypocone. The metacone is only slightly smaller and is closely joined to the hypocone by the posterior cingulum. With slight wear the two cusps become conjoined. The hypostyle is anteroposteriorly elongate in most specimens and is equal to the metacone in size. In most specimens it is set forward in relation to the rest of the metaloph and connected to the hypocone by the posterior cingulum. In several specimens the hypostyle is more in line with the rest of the metaloph.

M^1 is anteroposteriorly compressed with three well-developed roots. The protoloph is narrow, with the protocone set posteriorly from the paracone but connected to it by a short loph. The anterior cingulum passes from the internal margin of the paracone to the anteroexternal margin of the laterally compressed protostyle. A shallow valley is present between the anterior cingulum and the protocone, passing posteriorly between the latter and the protostyle to end in the transverse valley. The anterior valley is very short-lived, being obliterated in early wear. The transverse valley is deep and straight with closure of the lophs occurring first at the lingual styles and progressing labially from that point. In late wear there is no recognizable occlusal pattern except for the circular enamel band surrounding the occlusal part of the tooth with a slight labial inflection, an indication of the final junction of the two lophs.

There is only a slight difference between M^1 and M^2, with the difference in size being most noticeable. Second molars are smaller in all dimensions and the metaloph is obviously relatively shorter in M^2. M^2 also lacks the anterior cingulum, and the three cusps of the protoloph are aligned transversely across the loph. The transverse valley is as deep as on M^1 but is wider because the crescent-shaped metaloph slants posteriorly. Junction of the two lophs begins at the styles and progresses labially as on M^1, but the lophs remain distinct for a longer time due to the wide valley and deep labial sulcus extending almost to the base of the crown.

M^3 is the smallest and most variable of the dental battery. The tooth is essentially round in occlusal outline, with the hypostyle and protostyle showing various stages of fusion. The styles may be either free and completely separate at their apices or completely fused throughout their height. The protoloph is curved with a distinct protocone and paracone. The protocone is set posteriorly, and the anterior cingulum varies from complete (protostyle to paracone) to absent. The metaloph is concave throughout its length, with the cusps illustrating various stages in development. A shallow labial sulcus is present but is obliterated with wear, leaving only a deep central pit representing the transverse valley in later stages of wear.

The right mandible of the holotype is nearly complete, lacking only the coronoid process, condyle, and the most posterior part of the angle. The mandible is robust and deep. The diastema is shallow with a gently concave dorsal margin. The symphysis extends ventrally to produce a small "chin process." The masseteric scar is similar to that of other heteromyids, ending anteriorly in a small bony shelf anterior to the tooth row. Anteriorly, the shelf is nearly vertical in orientation and is continuous with a ventral ridge that curves posteriorly toward the angle of the mandible. The coronoid process is not preserved, but its base is clearly very small, indicating a delicate process, typical of heteromyids. The base of the lower incisor is marked on the ascending ramus as a posterolateral expansion of bone, just ventral to the coronoid process. The angle of the mandible appears broad and is medially inflected.

DP_4 is characterized by three pairs of cusps and an anterior ridge of cuspules. The two posterior cusps (hypoconid, entoconid) are joined near the center of the tooth by ridges which extend from the cusps anteriorly to a point between the next cusp pair. On the posterior margin of the tooth, a small cuspule (hypoconulid) exists between these two cusps as well as a labial cuspule (hypostylid). The middle pair of cusps is marginal with the lingual cusp (metaconid) being larger and not joined to any other cusp. The labial cusp (protostylid) joins the confluence of the crests from the posterior cusps. Anteriorly, a pair of laterally compressed cusps are joined to the concave anterior cingulum which has a series of cuspules on it.

P_4 is variable, especially in the configuration of the metalophid. The protostylid may be circular or ovate in occlusal outline and may be isolated from the remainder of the lophid until late wear. The metaconid is generally elongate and larger than the protostylid. The protostylid is more posterior than the metaconid. A small cuspule (anterostylid) is always present anterior and lingual to the protostylid, and is nearly equal in size to it. The protostylid and metaconid are connected with wear across the anterior border of the tooth. In some specimens, such as the holotype, a second anterostylid is present.

On the holotype a protoconid is formed lingual to the protostylid. The trigonid basin is a shallow enamel valley that persists until very late wear. The transverse valley is deep and slopes laterally and lingually from a point between the protoconid and hypoconid. With wear, the metalophid and hypolophid join laterally between these cusps. The hypolophid is relatively straight and bicuspid with a subequal hypoconid and entoconid. The two cusps are joined at their bases and in late wear become a single oval loph. On P_4 of the holotype a small hypostylid is present labial to the hypoconid. No other specimen shows this feature.

M_1 is nearly square in occlusal outline with the metalophid only slightly wider than the hypolophid. The protoconid and metaconid are subequal in size, but the latter is more anteroposteriorly compressed. The two cusps join at the anterior margin of the tooth at midheight of the cusps, at which point the anterior cingulum connects them with the small lateral protostylid. The cingulum makes a right angle toward the metaconid at the posterolabial corner of the tooth. A shallow valley begins at the anterolabial margin of the protoconid and then turns posteriorly between the protoconid and the cingulum–protostyle. Remnants of this valley are seen into late wear. The transverse valley is deep and straight but is relatively shallow at the stylids where it first closes. There is also a secondary closure of the valley in later wear between the metaconid and hypoconid. Three cusps comprise the hypolophid: a subequal hypoconid and entoconid joined at their centers, and a small lateral hypostylid. The result is an elongate oval hypolophid in early wear. The hypostylid is still discernible until late wear. CM 27958 and CM 27952 have a low posterior cingulum between the bases of the entoconid and the hypoconid. This structure is not seen on any of the remaining specimens.

M_2 is wider anteriorly than posteriorly. The protoconid and metaconid are essentially subequal, but the metaconid is anteroposteriorly compressed. The anterior cingulum terminates at the anterior margin of the protoconid and is continuous with the protostylid. A shallow valley is formed between the protostylid–anterior cingulum complex and the protoconid, and lasts until moderate wear as in M_1. The hypolophid consists of three cusps as on M_1. The hypostylid is variably developed and may be extremely weak on some specimens. The transverse valley is straight and deep, with primary union between the lophs occurring between the hypoconid and protoconid, giving a central connection. Secondary union occurs across the stylids. The hypolophid is lower than the metalophid, unlike M_1 in which both lophs are essentially the same height.

A characteristic feature of M_3 is the reduction in the hypolophid and to some extent the metalophid. The anterior cingulum is short and high, dropping very steeply into the transverse valley. The protoconid and metaconid are closely appressed to the apices and appear almost as one cusp with wear. The hypolophid is composed of two cusps which are quickly conjoined into one small crest. Junction of the lophs is central and, as in M_2, the hypolophid is much lower than the metalophid.

The partial postcranial skeleton included in the holotype preserves most of the right hindlimb, and some sacral and caudal vertebrae. In general proportions, the known skeletal elements of *Peridiomys halis* are more robust than that of Recent *Heteromys* and other heteromyids. In this way it is similar to the skeleton of the Clarendonian heteromyine "*Diprionomys*" *agrarius* described by Wood (1935). The limb elements of *P. halis* are also very close in size to those listed for "*D.*" *agrarius* (Wood, 1935:table III), but none of the long bones of the holotype of *P. halis* is complete, so no precise measurements can be taken. Unfortunately, no bones of the forelimb are preserved, so it cannot be determined whether there was a reduction of this limb with respect to the hindlimb as in other heteromyids.

Discussion.—*Peridiomys halis* is clearly referable to this genus based on its relatively low-crowned, robust cheek teeth, heteromyine pattern of wear on P^4 and P_4, and anteriorly flattened I_1. This species differs from the type species in having P_4 longer than wide (wider than long in *P. rusticus*) and consistently having a well-defined anterostylid on P_4. In some species of heteromyids the presence of accessory cuspules on P_4 is highly variable (Lindsay, 1972; Korth, 1979; Barnosky, 1986*a*). However, all specimens of *P. halis* have this cusp, and it is subequal in size to the other metalophid cusps, rather than appearing as a minute cuspule much smaller than the major cusps as in other heteromyids in which the occurrence of this cusp is variable. The holotype and only known specimen of *P. rusticus*, AMNH 18894, has a well-developed hypostylid on P_4 (Wood, 1935:fig. 97). Only the holotype of *P. halis* has this cusp on P_4.

Peridiomys halis is larger than all other species of the genus (Wood, 1935:table II; Storer, 1975:98). The skull of *P. halis* has a much deeper and longer rostrum than that of *P. oregonensis.* Both the upper and lower incisors of *P. oregonensis* are concave anteriorly and not anteriorly widened as in *P. halis* and other species for which the incisor is known (*Peridiomys* sp., *P. rusticus*). The less robust skull, mandible, and incisors of *P. oregonensis* suggest that it may not be referable to this genus.

Subfamily Perognathinae Coues, 1875
Genus *Perognathus* Maximillian, 1839
Perognathus ancenensis, **new species**
(Fig. 9, Table 9)

Holotype.—CM 28324, left P_4.

Referred Specimens.—CM 28503–28505, 28563–28564, 28573, maxillae with upper cheek teeth; KU 28583, 28683, 28684, isolated upper cheek teeth; KU 28657, CM 28370, 28352, isolated P_4s; CM 28479, 28481–28483, 28488, 28491–28492, isolated lower molars.

Horizon and Locality.—Anceney local fauna, center N 1/2, sec. 13, T2S, R3E, Madison Valley Formation, Gallatin County, Montana.

Age.—Early Barstovian (middle Miocene).

Diagnosis.—Differs from all other species of the genus in: union of lophs on P_4 buccal to center of tooth (between protostylid and hypoconid) instead of central; protostylid and metaconid of P_4 unite anteriorly rather than posteriorly; anterior cingulum continuous across entire width of M^1 and M^2 (not reduced as in *P. parvus*); lophs of lower molars do not unite across stylids; lophs of upper molars unite more readily across stylids than in other species.

Etymology.—Latin, *-ensis,* suffix denoting place or location; intended to refer to the Anceney fauna.

Description.—In general configuration, the teeth are low crowned and strongly rooted with well-developed cingula present on both upper and lower molars. The morphology of the teeth does not differ significantly from that of Recent specimens of *Perognathus parvus* from Wyoming and Utah except in size, development of the cingula, and slightly lower crowns.

P^4 is triangular in occlusal outline with a low, bulbous anterior protocone and convex metaloph composed of a large central hypocone, small lingual hypostyle, and an anteroposteriorly elongate metacone. The metaloph is well separated from the protocone (protoloph) and does not join until late wear, at which time the hypocone and protocone join centrally. The protocone has a distinct anterior bulge near its base before passing into a strong anteriorly directed root. Two other roots are present, one below the metacone and another beneath the hypostyle. Posterior cingula are variably developed either between the hypocone and hypostyle or between the hypocone and metacone.

M^1 is quadrate in shape with prominent anterior and posterior cingula developed. The tooth is sexicuspidate, forming two transverse lophs with wear. The cusps themselves are low and bulbous except for the protostyle and hypostyle, which are elevated and quickly incorporated into the cingula with wear. The transverse valley is therefore blocked lingually, with wear resulting in a U-shaped pattern opening labially. The transverse valley closes with wear from the lingual margin to the labial margin. The second molar is very similar to the first except that it is slightly more oval in shape, resulting from a closer appression of the protostyle and hypostyle as well as a slightly reduced metaloph. The last upper molar is rounded and has a reduced metaloph with the metacone existing only as a small protuberance on the labial end of the posterior cingulum. The hypostyle is also reduced in comparison to the protostyle.

Only four P_4s have been recognized as belonging to this species. Each has a widely separated and conical hypoconid and entoconid forming the hypolophid, and a closely set protostylid and metaconid. The anterior pair joins along the anterior border but remains distinct posteriorly. The two lophs show a tendency to unite labial of the center, between the protostylid and hypoconid. A single specimen (CM 28370) has a small cuspule between the hypoconid and entoconid (=?hypoconulid). The lower molars are quadrate as in the uppers but have reduced cingula. The anterior cingulum extends from the laterally compressed protostylid to join both the protoconid and metaconid. The protoconid is joined to the cingulum by a short crest while the metaconid is slightly compressed anteroposteriorly and narrowest as it meets the cingulum. The principal cusps are generally conical and separate at their

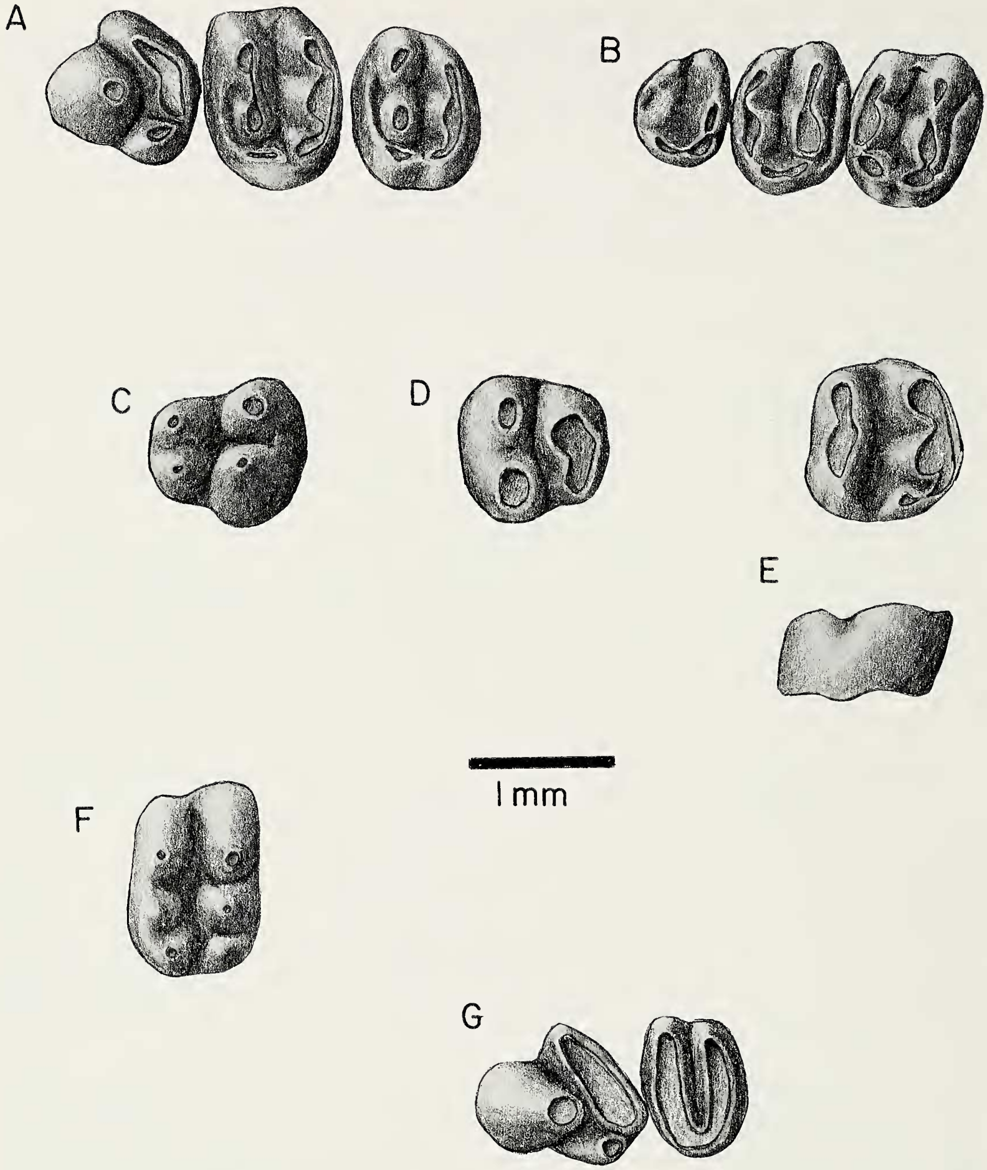


Fig. 9.—Dentitions of species of *Perognathus* and "*Mookomys*" cf. "*M.*" *formicarum* from the Anceney local fauna. A–E, *Perognathus ancenensis.* A, left P^4–M^2, CM 28503. B, right M^1–M^3, CM 28573. C, left P_4, CM 28324 (holotype). D, right P_4, CM 28352. E, right M_1 or M_2, CM 28479 (occlusal view above, buccal view below). F, "*Mookomys*" cf. "*M.*" *formicarum,* right M^1 or M^2, CM 28500. G, *Perognathus* sp. indet, left P^4–M^1, CM 28507.

bases. The transverse valley is straight and relatively deep remaining open across the occlusal surface even in late wear stages. If joining occurs, it will be between the protoconid and hypoconid rather than across the stylids as in the upper dentition. The hypolophid is straight and terminates in a variably developed hypostylid. The remainder of the lower dentition was not recognized in the sample although it is possible that M_1 and M_2 are represented here since they would be extremely similar in size and morphology.

Table 9.—*Dental measurements of* Perognathus ancenensis. *Measurements in mm. Abbreviations as in Tables 2 and 5.*

		n	$\bar{x}$	or	*s*	cv
P^4	a-p	3	0.95	0.93–0.96	0.01	1.49
	tra	3	0.47	0.45–0.52	0.03	7.02
	trp	3	1.01	0.96–1.10	0.06	6.53
M^1	a-p	4	0.91	0.87–0.93	0.02	2.69
	tra	4	1.15	1.09–1.19	0.04	3.60
	trp	4	1.14	1.09–1.19	0.04	3.19
M^2	a-p	2	0.83	0.80–0.86	—	—
	tra	2	1.08	1.05–1.10	—	—
	trp	2	1.04	0.98–1.10	—	—
P_4	a-p	4	1.07	1.03–1.11	0.03	2.72
	tra	4	0.71	0.68–0.80	0.05	7.14
	trp	4	0.95	0.89–1.00	0.04	4.10
M_1	a-p	7	1.04	1.00–1.12	0.05	4.62
	tra	7	1.12	1.07–1.21	0.04	3.86
	trp	7	1.08	1.00–1.14	0.06	5.21

Discussion.—Unique features of the cheek teeth of *Perognathus ancenensis* are the morphology of P_4 and the anterior cingula of the upper molars. The protostylid and metaconid of P_4 unite anteriorly, and the metalophid joins the hypolophid buccal to the center of the tooth, between the protostylid and hypoconid. In other species of *Perognathus* the cusps of the metalophid remain distinct anteriorly and merge posteriorly to unite with the center of the hypolophid (X-pattern of Wood, 1935).

The second diagnostic feature of *P. ancenensis* is the complete anterior cingulum on both M^1 and M^2. In some Recent and later Tertiary species of *Perognathus* the anterior cingulum is lost on M^2 and reduced to a small cuspule between the paracone and metacone on M^1 (Martin, 1984). The Barstovian species of *Perognathus, P. furlongi* and *P. brevidens,* maintain a complete anterior cingulum on M^1, but reduce the anterior cingulum on M^2. The only specimens of *Perognathus* that share this latter feature with *P. ancenensis* are teeth referred by Lindsay (1972) to *Perognathus minutus* from the Barstow Formation of California. These specimens are smaller than those referred to *P. ancenesis* (Lindsay, 1972: table 9). The upper molars of the Barstow sample maintain an anterior cingulum for nearly their entire width as in *P. ancenensis.*

In size, *Perognathus ancenensis* is closest to *P. furlongi* (Lindsay, 1972:table 9) and *P. brevidens* (Korth, 1979:table 1; Korth 1987:table 1). *Perognathus ancenensis* differs from these species in several important features. Besides the characters discussed above, *P. ancenensis* differs from *P. furlongi* in that the lower molars tend to wear without closing the transverse valley across the stylids. If wear does proceed to the point of extinction of the lophids, they tend to join centrally as in Recent *Perognathus.* In *P. furlongi* the union is across the stylids in very early wear in at least 50% of the known sample (Lindsay, 1972). The unique oblique connection of the lophids of P_4 in *P. brevidens* and its overall shortened and broadened shape are not shared with *P. ancenensis.*

Perognathus sp. indet.
(Fig. 9G)

Referred Specimen.—CM 28507, partial maxilla with left P^4–M^1.

Description.—P^4 is similar in size (a-p, 0.92 mm; tra, 0.46 mm; trp 0.95 mm) to *P. furlongi* (Lindsay, 1972:table 9) or *P. ancenensis* (Table 9). It has the typical inflated base of the protocone and enlarged anterior root with the metaloph composed of three cusps: an elongate metacone, central hypocone, and smaller rounded hypostyle. The hypocone and metacone are broadly joined due to the advancing wear of this specimen and the hypostyle has only recently joined the hypocone but is still discernible. The protocone is just beginning to show signs of joining the hypocone centrally. Except for a more vertical anterior root of P^4, there is little to distinguish this premolar from specimens of *Perognathus ancenensis.*

M^1, however, is quite distinctive in its small size, even though it is quite worn (a-p, 0.66 mm; tra, 0.87 mm; trp, 0.87 mm). The details of the cusp pattern have been worn away, but it appears to have had highly conjoined styles, and closure of the transverse valley has proceeded from the lingual margin progressively to the labial margin. In spite of the fact that *Perognathus* molars are somewhat tapered ventrally, the combined reduction from wear and taper is not enough to account for the small size of this tooth.

Discussion.—The species represented by CM 28507 cannot be readily referred to *Perognathus ancenensis,* primarily due to the small size of M^1 relative to the premolar. If the P^4 of CM 28507 were found isolated rather than associated with this small M^1, it would probably be identified as *P. ancenensis.* This situation is indeed unique since it appears that M^1 is smaller than P^4 in width. Generally, even in heavily worn dentitions of Recent and fossil *Perognathus,* M^1 and P^4 are of equal width or M^1 is slightly larger. P^4 is within the size range of *P. furlongi* or *P. ancenensis,* but M^1 is smaller than that in the smallest species of the genus, *P. minutus* (Lindsay, 1972:table 9) and *P. trojectioansrum* (Korth, 1979:table 2). Only less worn material will help to understand the true relationships of this small heteromyid.

Genus *Cupidinimus* Wood, 1935
Cupidinimus madisonensis (Dorr, 1956)
(Fig. 10, Table 10)

Perognathoides madisonensis Dorr, 1956.
Perognathoides halli Wood, Lindsay, 1972 (in part).
Cupidinimus madisonensis (Dorr) Barnosky, 1986*a*.

Holotype.—CM 8770, right mandible with P_4–M_2.

Referred Specimens.—CM 27979–27980, 27982–27986, 27989–27990, 27994, 27997–27999, 28006, 28465, KU 28544–28546, 28548–28540, 28552–28554, 28556, 28558–28561, maxillae with cheek teeth; CM 27886, 27992, 28000–28004, 28007–28015, 28017–28018, 28020, 28026–28027, 28029–28031, 28033–28037, 28039, 28041, 28043–28049, 28051–28055, 28057–28073, 28075, 28077–28078, 28081–28082, 28084–28088, 28092–28096, 28098–28099, 28101–28107, 28109, 28111–28116, 28119–28120, 28122, 28124–28127, 28128, 28130–28141, 28143–28147, KU 28541–28543, 28551, 28565–28568, 28570–28575, 28584–38597, 28599–28608, 28610, 28612, 28614–28616, 28618, 28650, P^4; CM 28024–28025, 28372, 28374–28381, 28387–28388, 28390–28401, 28405–28407, 28421–28427, 28430–28433, 28435–28444, 28446–28448, 28450–28451, 28454–28455, 28458–28464, KU 28576–28578, 28580, 28667–28670, 28672–28673, 28675, 28682, M^1; CM 28408–28410, 28412–28416, 28466, 28468–28474, 28498, 28511, KU 28671, 28677, M^2; KU 28581, M^3; CM 28506, 28519, 28521–28525, 28527–28528, 28530, KU 28678, 28679, 28680, mandibles with cheek teeth; CM 28305–28306, 28308–28309, 28311–28313, 28315–28323, 28325–28326, 28328, 28331–28337, 28339, 28341, 28343–28346, 28349–28350, 28354–28355, 28357–28258, 28360–28369, 28371, 28377–28378, 28512–28513, 28516–28518, KU 28653–28656, 28658–28662, 28664, 28666, P_4; CM 28148–28164, 28167–28174, 28176–28177, 28179–28193, 28195–28203, 28205, 28238–28248, 28253–28260, 28262, 28264–28265, 28267–28282, 28490, KU 28619–28629, 28637–28643, 28652, M_1; CM 28206–28214, 28216–28231, 28284–28302, KU 28630–28635, 28644–28648, M_2.

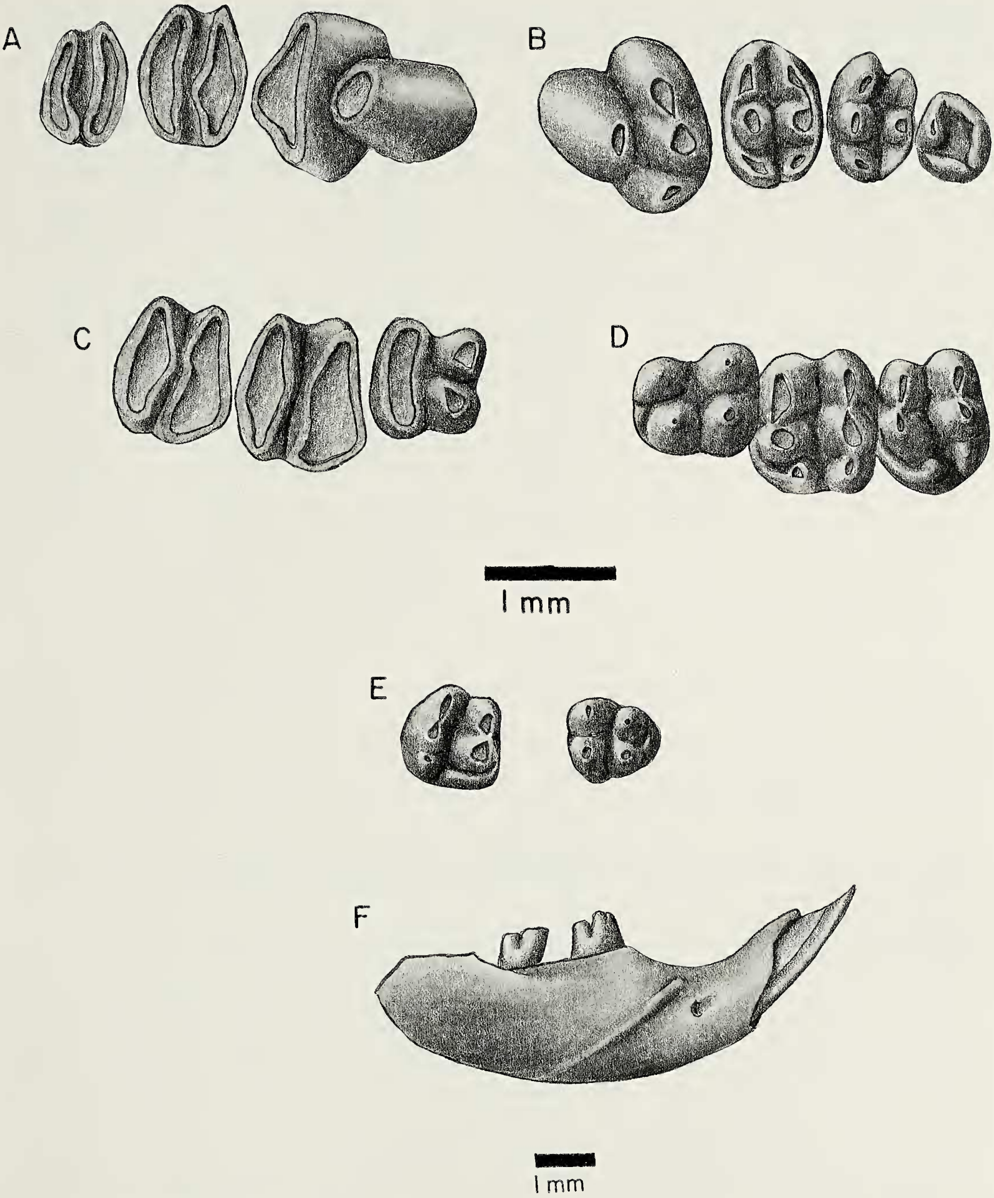


Fig. 10.—Dentitions of species of *Cupidinimus* from the Anceney local fauna. A–D, *Cupidinimus madisonensis.* A, right P^4–M^2, CM 27990. B, left P^4–M^3, CM 27984. C, right P_4–M_2, CM 8770 (holotype). D, left P_4–M_2, CM 28530. E–F, *Cupidinimus* cf. *C. eurekensis,* CM 28575. E, Occlusal view, right P_4, M_2. F, lateral view of mandible.

Horizon and Locality.—Anceney local fauna, center N 1/2, sec. 13, T2S, R3E, Madison Valley Formation, Gallatin County, Montana.

Age.—Early Barstovian (middle Miocene).

Emended Diagnosis.—Larger than *Cupidinimus eurekensis, C. lindsayi,* and *C.*

Table 10.—*Dental measurements of* Cupidinimus madisonensis. *Measurements in mm. Abbreviations as in Tables 2 and 5.*

		n	$\bar{x}$	or	s	cv
P^4	a-p	166	1.22	1.00–1.39	0.08	6.89
	tra	166	0.62	0.43–0.82	0.06	10.00
	trp	166	1.23	1.06–1.43	0.07	5.45
M^1	a-p	105	0.88	0.78–1.13	0.06	6.48
	tra	105	1.18	1.00–1.51	0.08	6.78
	trp	105	1.15	1.00–1.38	0.07	6.26
M^2	a-p	33	0.81	0.72–1.00	0.06	7.81
	tra	28	1.07	0.97–1.24	0.07	6.30
	trp	33	0.96	0.77–1.09	0.07	7.71
P_4	a-p	79	1.06	0.88–1.19	0.07	6.32
	tra	79	0.79	0.63–0.88	0.05	6.71
	trp	79	0.94	0.83–1.05	0.05	4.89
M_1	a-p	124	0.96	0.85–1.12	0.06	6.15
	tra	124	1.14	0.96–1.27	0.06	5.44
	trp	124	1.13	0.95–1.30	0.06	5.58
M_2	a-p	62	0.86	0.77–1.00	0.05	5.93
	tra	62	1.11	0.95–1.32	0.06	5.50
	trp	62	1.05	0.91–1.27	0.08	7.14

nebraskensis, smaller than all other species; cheek teeth relatively low crowned (equivalent to those of *C. lindsayi, C. whitlocki,* and lower crowned than *C. nebraskensis,* the type species); accessory cuspules occur on P_4 less frequently than in Great Plains species and more frequently than in *C. whitlocki* and more western species; hypostylid never present on P_4 as in *C. nebraskensis.*

Description.—P^4 is typical for heteromyids in its basic construction, being composed of an anterior pillar-like protocone and a metaloph composed of a metacone, hypocone, and hypostyle forming a convex loph behind the protocone. The protocone itself is generally somewhat flattened anteroposteriorly and may or may not have an accessory cuspule attach to it. If the cuspule is present it can be variably developed in that it may be a prominent cuspule remaining throughout much of the life of the tooth or it may be just a small cuspule near the crest of the protocone which is lost in early wear. The protocone itself does not fuse to the metaloph until considerable wear has occurred and when it does meet the metaloph it generally meets the center of the enlarged hypocone, although it may also meet lingual to this point between the hypocone and hypostyle. In rare instances it may fuse to the hypostyle as in heteromyines. The metaloph is composed of a large posterior hypocone which is closely conjoined to an anterior compressed metacone and a smaller, more rounded hypostyle which may or may not be joined to the hypocone by a posterior cingulum. The wear pattern on the tooth varies, presumably depending on the structure and occlusal action of the P^4.

M^1 is divided into two distinct lophs separated by a deep, straight transverse valley. The protoloph is composed of a laterally compressed protostyle from which the anterior cingulum passes in front of the protocone to connect with the anteroposteriorly compressed paracone. The protocone is conical and connects to the paracone after slight wear and to the anterior cingulum only in later wear. The metaloph is also three-cusped with a continuous posterior cingulum connecting the posterior margins of the hypostyle, hypocone, and metacone. As wear progresses, the lingual margin of the transverse valley closes first across the styles followed by a labially directed closure. The tooth is high crowned but rooted and is widest at the crown surface but tapers ventrally toward the roots.

M^2 differs from M^1 in its discontinuous anterior cingulum extending from the protostyle to the protocone and from the protocone to the metacone. Therefore, the protocone is not isolated as on M^1. The transverse valley is closed lingually and more sinuous, with secondary closure between the metacone and paracone, isolating an ephemeral internal basin. The metaloph is shorter than the protoloph, unlike M^1.

M^3 is considerably smaller than the preceding molars and is round in occlusal view. The protoloph is reduced to an anteroposteriorly elongated protostyle with a cingulum extending to the protocone.

The metacone is reduced to an anteroposteriorly elongate ridge connected to the protocone. The metaloph is low and continuous from the hypostyle through a ridge ending at the metacone. There are no distinct cusps evident on this ridge. The transverse valley is reduced to a central pit which persists until late wear.

The type mandible (CM 8770) is characterized by a diastema which is relatively flat but not as flat as that of *Mookomys altifluminis.* The masseteric crest is short and relatively low, extending from the level of the posterior margin of P_4, near the base of the mandible rising to middepth, just anterior to P_4. The mental foramen is round, just anterior and slightly below the terminus of the crest. The incisor is slightly rounded on its ventral margin. None of the ascending ramus is preserved in the type or in any of the referred material. Other specimens indicate that the masseteric crest may be stronger or weaker, and that the mental foramen may be slit-like or rounded and may occur more anteriorly than described above. The incisor may be more recurved and flattened ventrally.

P_4 is perhaps the most variable tooth in the series. In the type specimen, this tooth is badly worn but appears to have had four primary cusps uniting centrally after union of the two posterior cusps to form the hypolophid. In general, the metalophid is comprised of an anterior metaconid and more posteriorly placed protostylid, while the hypoconid and entoconid form the hypolophid. The most common configuration of these cusps results in the hypoconid and entoconid joining to form an anteroposteriorly compressed hypolophid, while the metaconid and protostylid do not unite but rather join with the hypolophid in the center of the transverse valley. Only late in wear will the anterior cusps unite at their centers. Variations on this theme seem to be unlimited. In many cases, small accessory cuspids are found in the center of the hypolophid (hypoconulid), anterior to the protostylid (anterostylid), or between the protostylid and metaconid (protoconid) which serves to unite the cusps of the metalophid anteriorly. The union of the lophs is not always central but sometimes is subcentral or even labial. The tooth is high crowned and rooted with a long vertical posterior root and anteriorly sloping anterior root. Posteriorly, the tooth is convex with the hypolophid slightly slanted anteriorly.

M_1 is equal to or slightly wider than P_4 and rectangular in occlusal outline. It is high crowned and rooted with the cusps uniting into lophs fairly early in wear. The protostylid is laterally compressed and gives rise to the anterior cingulum which runs directly anteriorly to the anteroexternal corner of the tooth, where it angles sharply to the internal margin of the tooth. It passes into the compressed metaconid and also joins the protoconid, forming the metalophid. As wear proceeds, a small valley between the protoconid and protostylid–cingulum complex remains open but closes just before the metalophid and hypolophid unite. The hypolophid is three-cusped and is composed of the subequal hypoconid and entoconid with a low, external hypostylid which does not unite with the hypoconid until relatively late wear, just before the transverse valley is blocked. This blockage usually occurs at the midpoint of the tooth by union of the two lophs between the hypoconid and the protoconid–metaconid complex. In some specimens the protostylid and hypostylid are closer together, essentially blocking the transverse valley, causing the first union of the lophs to be labial rather than central.

Discussion.—Dorr (1956) distinguished *Cupidinimus* (=*Perognathoides*) *madisonensis* from *C. halli* (Wood, 1936*a*) and other members of the genus by its small size and the presence of an anterior reentrant on the anterior face of P_4. As pointed out above, the latter character can be extremely variable due to the complexities of adding an extra cuspule to the tooth, a phenomenon quite common in *Cupidinimus.* Lindsay (1972) recognized this fact as well and indicated that *C. halli* also had an anterior reentrant on P_4, but further argued that *C. halli* and *C. madisonensis* were of the same size and were therefore synonymous. The measurements of *C. madisonensis* given by Dorr (1956:table 3) and those appearing in this paper (Table 10) place the species at the extreme low end of the range given for *C. halli* (Lindsay, 1972:table 9); in fact, Dorr's measurements fall outside the range given by Lindsay. Measurements of the entire sample from Anceney indicate that *C. madisonensis* is consistently smaller than *C. halli.* A statistical "t-test" was run on the anteroposterior measurements of the upper premolars and first molars of *C. halli* and *C. madisonensis.* All differences were significant at the .001 level. A test run on the transverse measurements of M_1 provided the same level of significance. The second lower molars are extremely similar in length. However, they are also quite variable in size within each species. The test showed no significance. Barnosky (1986*a*):fig. 10) measured the crown height of the lower molars of species of *Cupidinimus* and demonstrated that the molars of *C. madisonensis* were much lower crowned than those of *C. halli.* Lindsay (1972:56) noted that a minute hypostylid occurs on P_4 of many specimens of *C. halli* whereas this cuspule is not present on specimens from Anceney referred to *C. madisonensis.* Clearly *C. madisonensis* and *C. halli* are not be synonymous.

Cupidinimus sp., cf. *C. eurekensis* (Lindsay, 1972)
(Fig. 10E, F)

Referred Specimen.—CM 28575, mandible with right P_4 and M_2.

Measurements.–P_4: a-p, 0.69 mm; tra, 0.48 mm; trp, 0.59 mm. M_1: a-p, 0.69 mm; tra, 0.75 mm; trp 0.72 mm.

Description.—The mandible is complete from behind M_2 to the incisor. It is comparatively deep for its size, with a pronounced masseteric crest extending from the base of the jaw below the alveolus

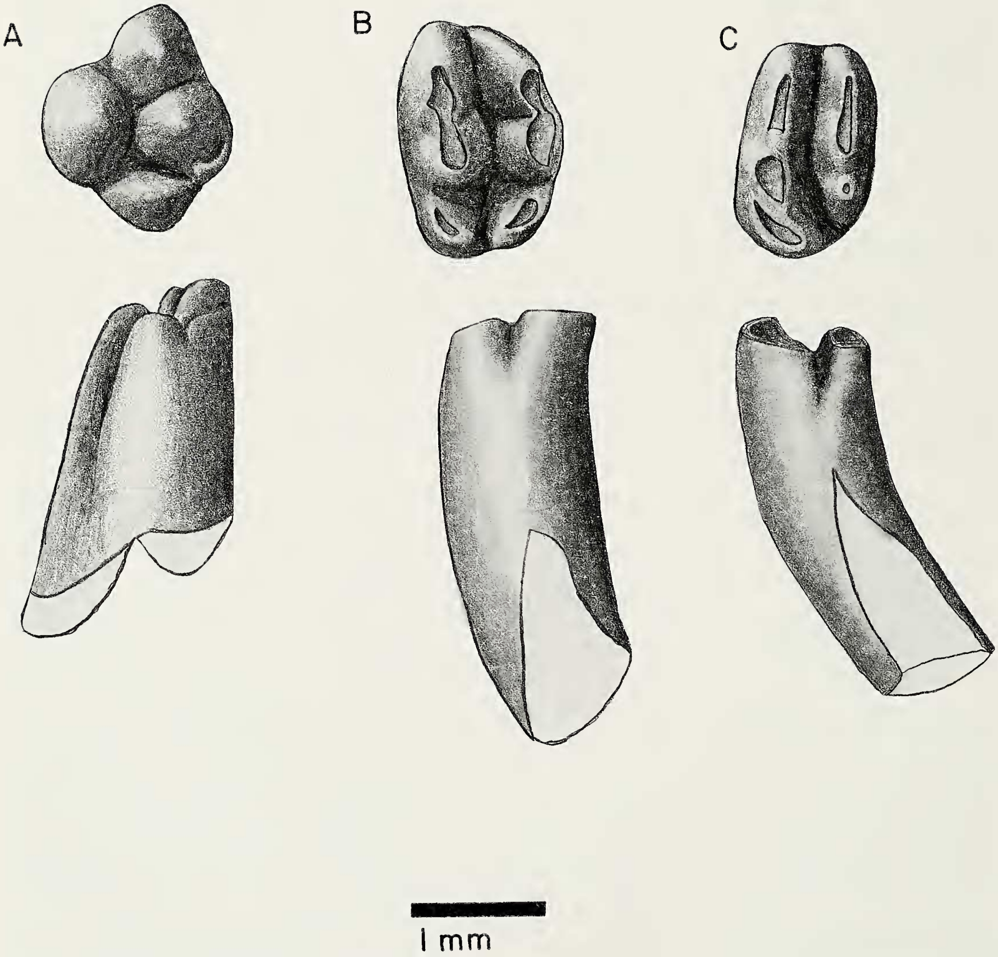


Fig. 11.—Isolated cheek teeth of *Phelosaccomys* cf. *P. annae* from the Anceney local fauna. A, left P^4, CM 27896 (lingual view below). B, left M^1 or M^2, CM 28404 (lingual view below). C, left M_1 or M_2, CM 28303 (buccal view below).

for M_1 in a straight line to just anterior to P_4 and below the dorsal margin of the diastema. The mental foramen is immediately anterior to the crest and just ventral to its terminus. The diastema is curved throughout its length, ending at a level above the occlusal surface of the cheek teeth. The ventral margin of the mandible is slightly arched. The incisor is moderately recurved, relatively wide, but not exceptionally deep anteroposteriorly.

Only two cheek teeth are present, P_4 and M_2. Both teeth are quite high crowned for the size of the animal. Occlusally, P_4 is composed of four cusps with the anterior pair smaller and more closely conjoined than the posterior pair. The protostylid and metaconid are joined posteriorly, and a valley opens anteriorly extending for only a short distance down the anterior face of the tooth. Neither cusp is more anteriorly positioned than the other. The posterior pair, hypoconid and entoconid, are subequal and only slightly compressed anteroposteriorly. The valley between them is deeper than that separating the anterior pair. The junction between the lophs will definitely be central since that is the highest point of the transverse valley from which it slopes steeply labially and lingually to end about midheight of the crown. Wear past this point would yield only a circular tooth of dentine ringed with enamel.

M_2 is also high crowned. The lophs persist for half of the enamel height. The metalophid typically shows the protoconid and metaconid joined anteriorly and uniting with the anterior cingulum, which extends from the laterally compressed protostylid. The cingulum extends anteriorly from the protostylid and arcs sharply lingually to join the metalophid. The hypolophid is straight and composed of a laterally compressed hypoconid and entoconid and a small lower hypostylid. All cusps on the tooth appear to wear fairly early into lophs. The transverse valley is straight, wide, and deep, with its first blockage probably occurring centrally, between the bases of the protoconid and hypoconid. What remains of the alveolus for M_3 appears to have contained a tooth with a single anteroposteriorly flattened root about half the size of M_2.

Discussion.—In size and crown height of the cheek teeth, CM 28575 cannot be distinguished from specimens of *Cupidinimus eurekensis* from the Barstow Formation of California (Lindsay, 1972). Barnosky (1986*a*:fig. 12) measured the crown height of the premolars of species of *Cupidinimus* and presented them as a ratio to the maximum width of the tooth (LEHP/T). The two P_4s referred by Lindsay (1972) to *C. eurekensis* yielded crown height ratios of 0.60 and 0.80. The P_4 of CM 28575 has a crown height ratio of 0.68, well within the range of the species.

The only factor barring CM 28575 from referral to *C. eurekensis* is the degree of wear on the holotype and topotypic specimen from California (UCMP 78164, UCMP 78165). Both of these specimens have lost the occlusal pattern of cusps on the cheek teeth (Lindsay, 1972:fig. 29) so no comparison can be made between them and CM 28575, which preserves the occlusal morphology without wear. Additional unworn specimens from the type area for *C. eurekensis* are necessary for a definite allocation of the Anceney specimen to this species.

Family Geomyidae Bonaparte, 1845
Subfamily uncertain
Genus *Phelosaccomys* Korth and Reynolds, 1994
Phelosaccomys sp., cf. *P. annae* (Korth, 1987)
(Fig. 11, Table 11)

Lignimus cf. *L. hibbardi* Storer, Korth, 1979.
Parapliosaccomys annae Korth, 1987.
Phelosaccomys annae (Korth) Korth and Reynolds, 1994.

Referred Specimens.—CM 28022, partial maxilla with left M^1–M^2; CM 27896, isolated P^4; CM 28389, 28404, 28411, 28418, isolated upper molars; CM 28165–28166, 28204, 28250, 28263, 28303, KU 28631, 28649, isolated lower molars.

Description.—The cheek teeth of this species are all high crowned, rootless, and exhibit enamel failure both laterally and lingually. Enamel failure is variably developed, being less distinct on the upper premolar.

P^4 is subequal in size to M^1. The protocone is a transversely elongate oval. The metaloph consists of three cusps and is slightly convex posteriorly. The central hypocone is the largest cusp. The hy-

Table 11.—*Dental measurements of* Phelosaccomys *cf.* P. annae *from the Anceney local fauna. Measurements in mm. Abbreviations as in Tables 2 and 5.*

		n	$\bar{x}$	or	*s*	cv
P^4	a-p	1	1.54	—	—	—
	tra	1	0.84	—	—	—
	trp	1	1.69	—	—	—
M^1	a-p	3	1.14	1.09–1.19	0.04	3.0
	tra	3	1.69	1.65–1.75	0.04	2.6
	trp	3	1.62	1.51–1.66	0.05	3.0
M^2	a-p	3	1.06	1.00–1.10	0.04	4.1
	tra	3	1.46	1.40–1.52	0.05	3.4
	trp	3	1.25	1.22–1.30	0.04	2.8
M_1	a-p	5	1.18	1.13–1.23	0.04	3.2
	tra	5	1.53	1.45–1.62	0.06	3.9
	trp	5	1.55	1.48–1.59	0.04	2.4
M_2	a-p	3	0.98	0.95–1.04	0.04	4.1
	tra	3	1.40	1.32–1.54	0.10	7.2
	trp	3	1.33	1.30–1.38	0.04	2.8

postyle is positioned slightly anterior to the rest of the metaloph and union with the protocone will be with the anterior end of the hypostyle. A small posterior cingulum originates at the apex of the hypocone and extends lingually but stops before joining the hypostyle. It appears that this cingulum will disappear in very early stages of wear.

M^1 is composed of two nearly subequal lophs, each composed of three cusps. The protostyle and hypostyle effectively block the lingual exit of the transverse valley in relatively unworn specimens. The protostyle is connected to the paracone by a thin and ephemeral anterior cingulum which does not contact the protocone. The protocone connects directly to the paracone. The metaloph is composed of three cusps which are almost linearly aligned. The transverse valley is shallowest lingually and deepest labially, but the entire occlusal pattern is very shallow and is quickly lost with wear. M^2 is similar to M^1 except that the styles are fused to block completely the transverse valley, and the metaloph is more convex. The shaft of the tooth is also more curved than in M^1.

The lower molars are also high crowned. Enamel failure is also present and the occlusal pattern is very shallow. The metaconid of M_1 is anteroposteriorly compressed with the protoconid rounded. Both cusps are connected to the anterior cingulum, which is weak anteriorly but strong as it extends forward from the protostylid. The hypolophid is linear and the hypostylid is the last cusp to be fully incorporated into the loph, as it is slightly smaller and lower than the hypoconid and entoconid. Junction of the lophs is central, extending to the labial margin shortly after wear. The labial margin of the transverse valley is the last to close.

Discussion.—In all observable features, the specimens from Anceney are identical to the topotypic material of *Phelosaccomys annae* from the late Barstovian of Knox County, Nebraska, except for being slightly smaller (Korth, 1979:table 5, 1987:table 1). The degree of hypsodonty of the cheek teeth is nearly identical to that of *P. annae,* slightly higher than the unnamed species from the middle Barstovian of Brown County, Nebraska (Voorhies, 1990*a*), and lower than that of *P. shotwelli* from the Clarendonian of California.

Family Cricetidae Rochebrune, 1883
Genus *Copemys* Wood, 1936*b*
Copemys lindsayi, **new species**
(Fig. 12, Table 12)

Holotype.—CM 27711, right mandible with M_1–M_2.

Referred Specimens.—CM 27709, 27710, 27713–27715, upper dental elements; CM 27712, 27716, 27717, 27864, 27865, KU 28391, lower dental elements.

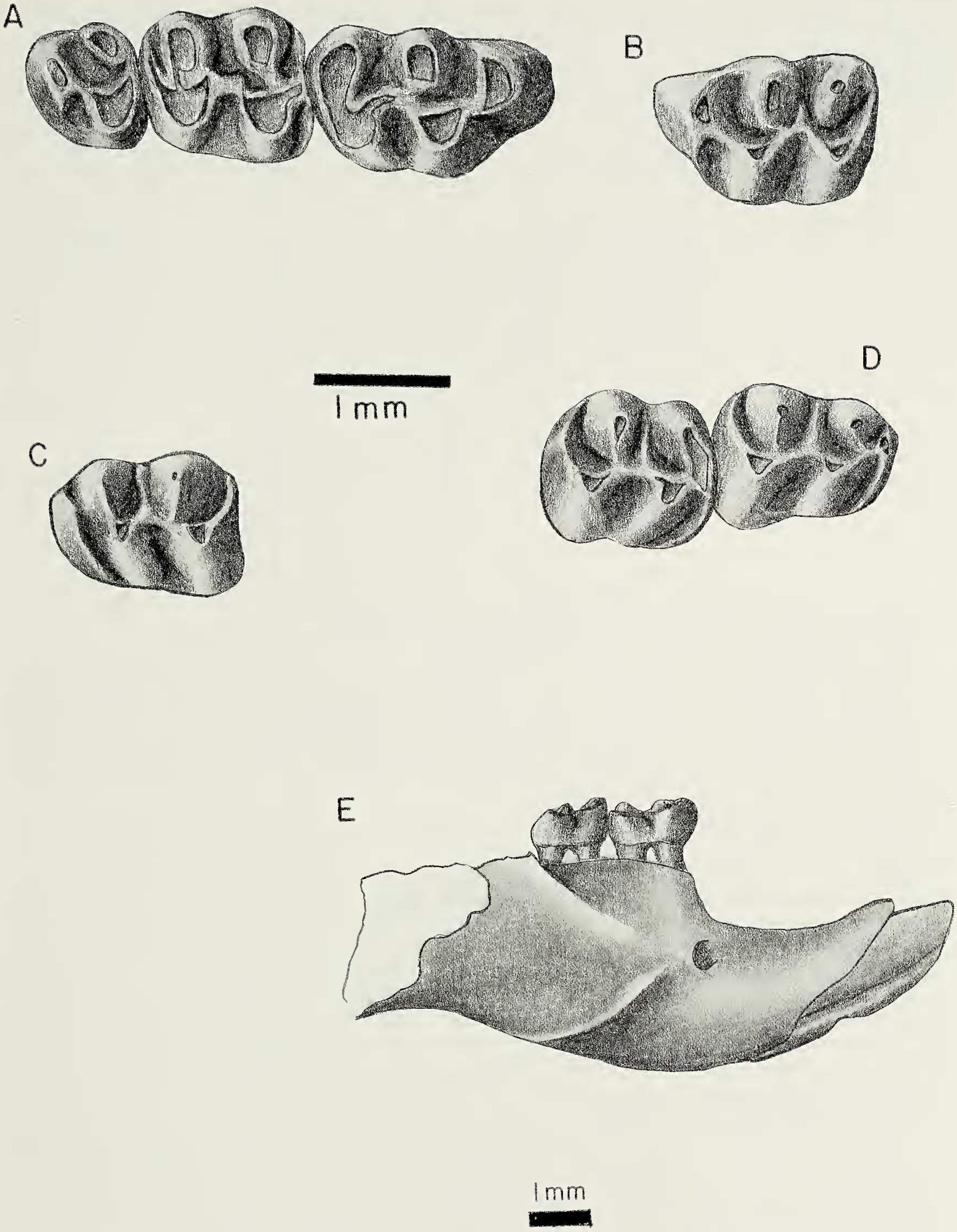


Fig. 12.—Mandible and dentitions of *Copemys lindsayi*. A, right M^1–M^3, CM 27709. B, left M^1, CM 27710. C, left M_1, CM 27717. D–E, CM 27711 (holotype). D, right M_1–M_2. E, Lateral view of mandible.

Table 12.—*Dental measurements of* Copemys lindsayi. *Measurements in mm. Abbreviations as in Tables 2 and 5.*

		a-p	tra	trp
M^1	CM 27709	1.65	0.99	1.00
	CM 27710	1.53	1.00	1.10
	CM 27713	1.60	1.10	1.11
	CM 27714	1.65	1.13	1.11
M^2	CM 27715	1.17	1.13	0.98
	CM 27709	1.27	1.11	1.03
M^3	CM 27709	0.09	0.97	
M_1	CM 27711	1.28	0.95	1.06
	CM 27712	1.28	0.86	0.96
	CM 27717	1.34	0.84	0.99
	CM 27864	1.36	0.89	1.10
M_2	CM 27716	1.29	0.97	1.00
	KU 28391	1.23	0.93	0.89
	CM 27865	1.24	0.95	0.99
	CM 27711	1.24	1.04	1.10
	CM 27712	1.17	0.99	0.96

Horizon and Locality.—Anceney local fauna, center N 1/2, sec. 13, T2S, R3E, Madison Valley Formation, Gallatin County, Montana.

Age.—Early Barstovian (middle Miocene).

Diagnosis.—Smallest species of the genus; similar to *C. pagei* in morphology, differing only in its smaller size and lacking a long anterior arm of the protoconid. Differs from other species in lacking a paralophule on M^1; and having mesolophs of differing lengths on the upper molars (intermediate on M^1, long on M^2); mesoloph is long on M_1 as in *C. pagei.*

Etymology.—Patronym for E. H. Lindsay in recognition of his detailed work on later Tertiary cricetids.

Description.—The first upper molar is constricted anteriorly in the area of the anterocone but the remainder is of equal width. The anterocone is labially displaced and slopes steeply to join the base of the protocone and paracone on the margins of the tooth. The paracone slopes posteriorly and does not connect to the anterocone itself but meets the posterior arm of the protocone at the midline of the tooth. The anterior arm of the protocone connects medially with the anterocone but the paracone is isolated from the anterocone and joins the posterior arm of the protocone on the midline of the tooth. The mesoloph varies in length but usually reaches about halfway to the lingual margin. One specimen (CM 27714) is completely unworn and has a small but distinct mesostyle. Posteriorly, the metacone is also isolated but may connect to the posterior cingulum by a narrow metalophule in unworn specimens. The posterior cingulum slopes downward from the hypocone and past the metacone to end at the posterolingual corner of the tooth.

M^2 is square in occlusal outline with the posterointernal corner being slightly rounded, narrowing the posterior width of the tooth. The anterior cingulum is straight and runs the entire anterior margin of the tooth. At the center of the anterior cingulum, the anterior arms of the protocone and paracone intersect. The posterior arms of these cusps also meet at the midline as on M^1. The mesoloph is complete and ends lingually in a mesostyle. The metacone is connected to the hypocone by a low, thin metalophule and the posterior cingulum is completely isolated from the metacone.

M^3 is represented by a single worn specimen and little of the occlusal detail is distinguishable. The shape is roughly triangular because the posterior half of the tooth is reduced. The labial margin is complete, but the metacone is rotated posterointernally to lie almost on the midline of the tooth. The protocone appears to be unreduced; however, the anterior cingulum is compressed against these cusps. The hypocone is apparently absent on M^3 or at best only slightly developed.

Two fragments of mandibles were recovered but both are broken anterior to the ascending ramus. The masseteric fossa is well defined and terminates below the posterior root of M_1. The diastema slopes strongly downward in front of the molar and is relatively flat anteriorly, arching only slightly dorsally at the anerior end to terminate below the level of the alveolar line. The mental foramen is relatively large and round, located just anterior to the anterior root of M_1 and close to the dorsal margin of the diastema just below the steepest downward slope. The mandible is very deep, giving the impression of a massive, somewhat compressed jaw. The ascending ramus originates at the level of M_2 and appears to rise rather steeply.

In the holotype, part of the incisor is preserved. The incisor is laterally compressed and the ventral surface is smooth with no evidence of any grooving or striations as are common in some of the earlier cricetids.

M_1 is elongate and slightly narrower than M_2. The anteroconid is prominent and connected to the metaconid and protoconid either by a single lophid which bifurcates or by individual lophids from the cusps meeting at the anteroconid. The anterior cingulum curves posteriorly from the anteroconid and descends to the base of the protoconid. The metaconid and anteroconid are separated by a notch which varies in depth. The posterior arm of the protoconid meets the anterior arm of the hypoconid in the center of the tooth, the two arms forming a V-shape. From this point, a mesolophid extends to the lingual margin of the tooth except in CM 27864, which has a short mesolophid. A short hypolophid connects the entoconid to the anterior arm of the hypoconid. The posterior arm of the hypoconid is continuous with the posterior cingulum, which ends at the posterointernal corner of the tooth.

M_2 is very similar to M_1 except for the anterior margin, which has no anteroconid but rather an anterior cingulum. The anterior cingulum is joined to the internal margin of the metaconid and passes straight across the anterior margin. It curves at the anteroexternal corner of the tooth and descends to the base of the protoconid. The curve is sharper in M_2 than M_1, giving the anterior half of the tooth a more squared appearance than in M_1.

There are no third molars present in the collection, but from the alveolus preserved in the holotype, M_3 appears to have been subequal in length to M_2, but narrower posteriorly.

Discussion.—*Copemys lindsayi* is the smallest species of the genus (see Clark et al., 1964:table 4; Shotwell, 1967:table I; Lindsay, 1972:table 12). Besides size, it differs in occlusal pattern of the cheek teeth from other Barstovian species of the genus. It differs from *C. russelli, C. loxodon,* and *C. niobrarensis* (=*C. kelloggae*) in lacking a well-developed paralophule on M^1. It also differs from *C. russelli* in lacking a weakly bilobed anterocone on M^1. *Copemys lindsayi* differs from *C. longidens* in having longer mesolophs (-ids) on M^2 and the lower molars. *Copemys lindsay* differs from *C. barstowensis* and *C. esmeraldensis* in having less robust cusps and lacking the transversely elongate, asymmetrical (sometimes bilobed) anterocone on M_1. *Copemys lindsayi* is closest in morphology to *C. pagei* but differs from it in lacking the long anterior arm of the protoconid of M_1 present in the latter.

Lindsay (1972) listed *Tregomys shotwelli* Wilson (1968) from the Clarendonian of Kansas as a species of *Copemys.* This species is very close in size to *C. lindsayi.* However, *T. shotwelli* differs from all species of *Copemys* in the morphology of M_1 by having a central, symmetrical anteroconid and a protoconid and metaconid that are aligned directly opposite one another, rather than showing the beginnings of alternation as in *Copemys.* The molars of *Tregomys* also lack mesolophs (-ids) and any accessory lophules that are common in species of *Copemys. Tregomys* is not synonymous with *Copemys.*

Voorhies (1990*a*) also pointed out a number of differences in the morphology of the mandible of *Tregomys* and *Copemys.* The morphology of the mandible of *C. lindsayi* is typical for species of *Copemys.*

CONCLUSIONS

Dorr (1956) suggested that the age of the Anceney local fauna was late Barstovian or earliest Clarendonian based on the species he recognized in the fauna (see Table 1). Among the rodents, a number of the genera present are typical of other Barstovian faunas but are not necessarily limited to the Barstovian: *Cupi-*

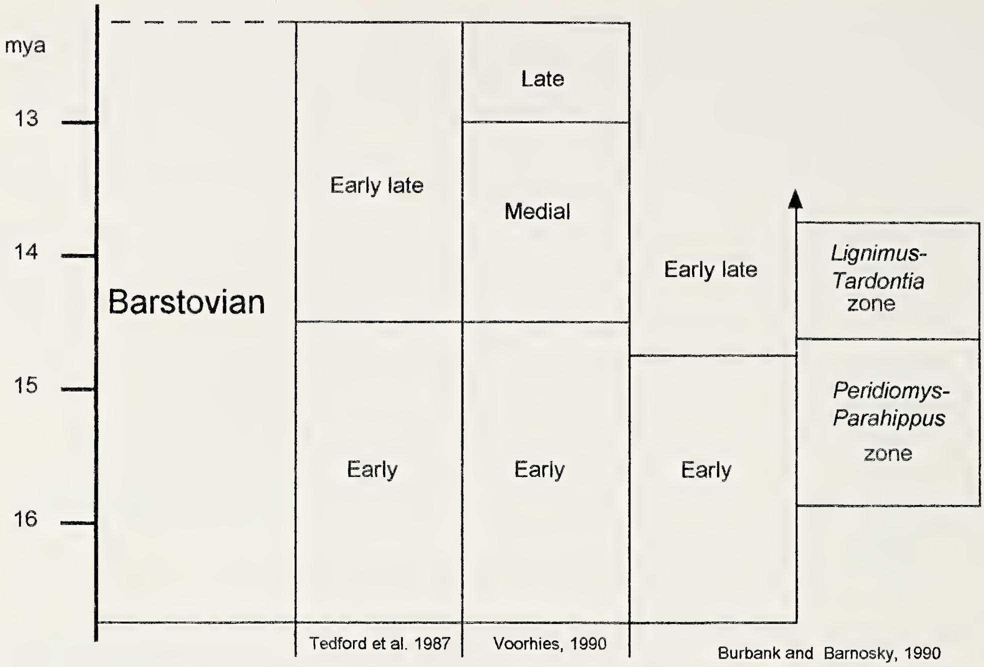


Fig. 13.—Divisions of the Barstovian proposed by previous authors.

dinimus, Copemys, Peridiomys, Phelosaccomys, and *Perognathus.* The combination of these genera indicates that the Anceney fauna is clearly Barstovian in age as suggested by Dorr (1956).

Tedford et al. (1987) divided the Barstovian into early and late intervals. In turn, they divided the late interval into two intervals, early late Barstovian and late late Barstovian. Voorhies (1990*b*) recognized three levels in the Barstovian (early, middle, late) but allocated Tedford's late late Barstovian interval to the early Clarendonian and included his middle and late Barstovian intervals in what Tedford et al. (1987) considered their early late Barstovian (Fig. 13).

Two heteromyid genera that are present in the Anceney fauna, *Peridiomys* and *Mookomys,* are also typical of earlier Barstovian and Hemingfordian, respectively. Munthe (1988) listed the former genus from the Hemingfordian of Wyoming. The beaver from Anceney, *Euroxenomys inconnexus,* most closely resembles "*Monosaulax* n. sp." from the Hemingfordian of northeastern Colorado (Wilson, 1960). The combination of these taxa suggests an earlier Barstovian age for the fauna.

On the species level, two species present at Anceney are known only from early Barstovian horizons. The holotype and all referred specimens of *Mylagaulus vetus* are from the latest Hemingfordian Split Rock fauna of Wyoming or earliest Barstovian Sheep Creek Formation in Nebraska. The common mylagaulids of all other described middle and late Barstovian faunas from the Great Plains are *M. laevis* or *M. monodon* (Gazin, 1932; Storer, 1975; Voorhies, 1990*a,* 1990*b*). Both of these later species are larger and have more complex occlusal patterns on the cheek teeth than *M. vetus.*

Cupidinimus eurekensis is known only from the lower levels of the Barstow

Table 13.—*Mammalian faunal list of Anceney local fauna. * indicates species exclusive to the Anceney fauna.*

- Insectivora
  - Erinaceidae
    - *Brachyerix incertis*
  - Soricidae
    - *Limnoecus* n. sp.*
    - *Angustidens* cf. *A. vireti*
  - Talpidae
    - *Domninoides* n. sp.*
- Chiroptera
  - Vepertilionidae
    - *Ancenycteris rasmusseni*
- Lagomorpha
  - Ochotonidae
    - *Oreolagus nevadensis*
  - Leporidae
    - *Hypolagus* sp.
    - genus and species indet.
- Rodentia
  - Mylagaulidae
    - *Trilaccogaulus bettae**
    - *Mylagaulus vetus*
  - Sciuridae
    - *Tamias* near *T. ateles*
    - *Spermophilus* (*Otospermophilus*) *jerae**
    - ?*Cynomys* sp. indet.
  - Castoridae
    - *Monosaulax* cf. *M. curtus*
  - Heteromyidae
    - *Mookomys thrinax**
    - "*Mookomys*" cf. "*M.*" *formicarum*
    - *Peridiomys minutus**
    - *Peridiomys halis**
    - *Perognathus* sp. indet.
    - *Perognathus ancenensis**
    - *Cupidinimus madisonensis*
    - *Cupidinimus* cf. *C. eurekensis*
  - Geomyidae
    - *Phelosaccomys* cf. *P. annae*
  - Cricetidae
    - *Copemys lindsayi**
- Carnivora
  - Canidae
    - *Tomarctus temerarius*
    - *Aelurodon* cf. *A. wheelerianus*
  - Mustelidae
    - *Plionictis ogygia*
    - *Martes* cf. *M. kinseyi*
    - ?*Mionictis* sp.
    - *Leptarctus primus*
- Perissodactyla
  - Equidae
    - *Hypohippus* cf. *H. osborni*
    - *Merychippus* cf. *M. intermontanus*
  - Tapiridae
    - Genus and species indet.
  - Rhinoceratidae
    - *Peraceras ceratorhinus*
- Artiodactyla
  - Merycoidodontidae
    - ?*Ticholeptus* sp.
  - Camelidae
    - Stenomyline, genus and species indet.
  - Moschidae
    - *Blastomeryx* cf. *B. elegans*
  - Antilocapridae
    - *Merycodus* cf. *M. necatus*

Formation in southern California (base of *Pseudadjidaumo stirtoni* zone), again suggesting an early Barstovian age for the Anceney fauna (Lindsay, 1972:fig. 37).

The remainder of the fauna (Table 13) reflects an age similar to that of the rodents. The majority of the species are typical of, though not necessarily restricted to, the Barstovian, and a few species suggest an early to middle Barstovian age for the fauna. The soricid *Aleurodon vireti* is known elsewhere only from the Hemingfordian (Wilson, 1960), and the ochotonid *Oreolagus nevadensis* is limited to the early Barstovian (Dawson, 1965). These occurrences also suggest an early Barstovian age.

The first occurrence of proboscideans is a distinctive marker for the late Barstovian of Tedford et al. (1987) and middle Barstovian of Voorhies (1990*b*). There are no proboscideans in the Anceney fauna, supporting an early Barstovian age for the fauna. However, since the majority of the fauna is composed of micromammals and larger mammals are relatively rare, the lack of proboscideans may be an artifact of the taphonomy of the fossil quarry rather than a true absence.

Presence of the canid *Aleurodon wheelerianus* in the Anceney fauna is problematical. Tedford et al. (1987) listed the first occurrence of the genus *Aleurodon* in North America as coincident with the first occurrence of proboscideans, at the beginning of the late Barstovian (=middle Barstovian of Voorhies, 1990*b*). The remainder of the fauna suggests an early Barstovian age for the Anceney fauna, whereas the occurrence of *Aleurodon* suggests a middle Barstovian age. This occurrence may indicate that the Anceney fauna is near the boundary between the early and middle (or early late) Barstovian.

Burbank and Barnosky (1990:fig. 9) defined faunal zones for the Barstovian of the northern Rocky Mountains based on the mammalian fauna from the Hepburn's Mesa Formation of Montana. They defined two zones, an earlier *Peridiomys–Parahippus* zone (early Barstovian) and a later *Lignimus–Tardontia* zone (early late Barstovian). They suggested that the Anceney fauna was equivalent to the lower part of the *Lignimus–Tardontia* zone, making the Anceney fauna early late (or middle) Barstovian in age.

However, the Anceney fauna does not easily fit into the definitions of these zones. First, the Anceney fauna lacks nine of the 16 rodent and insectivore taxa used by Burbank and Barnosky (1990): *Mesoscalops, Petauristodon, Mesogaulus douglassi, Tardontia, Diprionomys, Lignimus, Leptodontomys* (=*Pseudadjidaumo*), *Pseudotheridiomys, Schaubeumys.* This reduces the number of taxa that can be compared. Of the taxa listed as restricted to the upper zone, five are present in the Anceney fauna: *Spermophilus, Tamias, Perognathus, Cupidinimus,* and *Copemys.* However, all of these genera except *Spermophilus* have been reported from early Barstovian or Hemingfordian faunas in other parts of North America. Among the taxa restricted to the earlier *Peridiomys–Parahippus* zone, *Hypolagus* and *Merychippus* are present in the Anceney fauna. *Merycodus* is present in the Anceney fauna and it ranges from the top part of the *Peridiomys–Parahippus* zone to the very lowest part of the *Lignimus–Tardontia* zone. This combination of taxa limited to the upper zone along with taxa restricted to the lower zone makes placement of the Anceney fauna in this scheme nearly impossible. If, as suggested by Burbank and Barnosky (1990), the upper faunal zone is equivalent to the early late Barstovian of Tedford et al. (1987), which is characterized by the presence of proboscideans, then the lack of proboscideans suggests an early Barstovian age for the Anceney fauna.

The Anceney local fauna appears to be later early Barstovian in age, roughly correlating with the faunas from the Olcott (=Lower Snake Creek) Formation of Nebraska (Matthew, 1924), Flint Creek fauna from Montana (Black, 1961), and the Mascall fauna from Oregon (Downs, 1956).

The Anceney rodent fauna lacks a number of genera that appear to be geographically limited. The Barstovian faunas from the Great Plains consistently contain zapodids, the heteromyid "*Diprionomys*" *agrarius,* and the geomyoid genus *Lignimus* (Storer, 1975; Voorhies, 1990*a*; Korth, in press) that are generally absent in Barstovian faunas from the far west (Gazin, 1932; James, 1963; Shotwell, 1968; Lindsay, 1972). Similarly, the genus *Mojavemys* is present in the western faunas (Lindsay, 1972) but lacking in faunas from the Great Plains. Based on these occurrences, the Anceney fauna has greater homotaxial similarity to the faunas from the west than to those from the Great Plains.

Another Barstovian fauna reported from the Rocky Mountain area is that from the Colter Formation of Wyoming (Barnosky, 1986*b*). The Wyoming fauna is different from the Anceney fauna in containing elements of both the western faunas (*Mojavemys*) and the Great Plains faunas (*Lignimus*, "*Diprionomys*" *agrarius*, and zapodids) that are lacking in the Anceney fauna. It appears that the Colter Formation fauna represents an area of overlap between the western and eastern Barstovian faunas and the Anceney fauna is more closely related to the western faunas.

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